Effects of Food and Vegetation on Breeding Birds and Nest Predators in the Suburban Matrix

DISSERTATION

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By

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Abstract

The expansion of urbanization globally has prompted scientists to examine the effects of human developments on wildlife communities, often using birds as focal taxa. Most studies in this vein of research describe the patterns of avian response to urbanization, usually within habitats protected from human development, or among habitats varying in development pressure. The paucity of studies within the suburban matrix leaves us with a large gap in understanding of the effects of urbanization on birds. Moreover, the underlying processes driving the observed patterns remain poorly understood.

My research investigates population- and community-level consequences of anthropogenic food and vegetation resources in the suburban matrix, focusing on breeding birds and their nest predators. I combine observational and experimental approaches to test how anthropogenic subsidies and habitat modification affect avian population demography and predator-prey interactions, and compare these patterns between developed (i.e. residential yards) and undeveloped (i.e. forested parks) areas within suburban landscapes.

My study system is the Columbus, Ohio metropolitan area, where colleagues and I have investigated the influence of urbanization on songbirds since 2001. Whereas previous studies in the system focused exclusively on riparian forest parks, my

dissertation project extended research into the suburban matrix adjacent to seven of the long-term forest study sites. I used two focal species, American robin (*Turdus migratorius*) and northern cardinal (*Cardinalis cardinalis*), that are the most common songbirds that nest in residential yards and adjacent forest parks. Both robins and cardinals are native species that build open-cup nests in understory and midstory vegetation. However, these two species differ in respect to other life history characteristics such as size and diet.

The first component of my research addressed the common perception that matrix habitats within cities fail to provide quality breeding opportunities to birds. This is an important issue given the growing interest in managing the residential matrix to support biodiversity conservation. I evaluated differences in nesting success of robins and cardinals in riparian forest parks and adjacent residential neighborhoods during April-August 2011-2014. I specifically tested if nest predation was higher in residential yards versus forest parks, and identified which species were responsible for nest depredations in each habitat. Both robins and cardinals experienced similar nest survival rates in residential yards and forest parks, but there were clear differences in which species were responsible for depredation events. Specifically, domestic cats (*Felis catus*) were over 5x as frequently documented depredating cardinal nests in yards versus forest parks. My results suggest that at least in some circumstances, nest success of native birds may be equivalent between nature reserves and adjacent residential matrix habitats. Thus, residential areas can contribute to the conservation of native birds.

The second component of my research addressed how changes in resource

availability associated with urban development might affect habitat suitability for wildlife in cities and impact species interactions. Although some of these changes are unintentional, other habitat alterations are deliberate and intended to benefit urban wildlife, particularly songbirds. I tested the hypothesis that wildlife-friendly gardening programs that promote planting trees and shrubs (i.e. increasing woody cover) have the unintended consequence of attracting predators of avian nests. To test this, I examined relationships between woody vegetation cover and diurnal activity patterns of five nest predators that are common in suburban neighborhoods. I surveyed predator activity and characterized habitat using aerial imagery of seven suburban neighborhoods during April – August 2011 and 2012. Predator activity varied widely among individual yards, but contrary to my hypothesis, the availability of woody cover at either yard or neighborhood scales was not a strong predictor of diurnal activity in yards for Eastern gray squirrel (*Sciurus carolinensis*), common grackle (*Quiscalus quiscala*), brown-headed cowbird (*Molothrus ater*), blue jay (*Cyanocitta cristata*), or domestic cat (*Felis catus*). My findings suggest that the vulnerability of songbird nests to predation may not rise with increased availability of woody cover in yards and neighborhoods, and thus support recommendations to plant trees and shrubs to improve the residential matrix for songbirds.

The third component of my work focused on anthropogenic foods, which despite being pervasive in urban landscapes, are poorly understood in terms of their effects on species interactions. I used observational and experimental approaches to investigate how the most common subsidy, bird feeders, affected predator-prey dynamics in between

songbirds and nest predators in the residential matrix. From April-August 2011-2014, I quantified bird feeders, nest survival of robins and cardinals, and numbers of six common nest predators: Eastern gray squirrel, common grackle, brown-headed cowbird, blue jay, domestic cat, and American crow, *Corvus brachyrhynchos*. Species responded differently to anthropogenic subsidies. Bird feeders were positively associated with diurnal activity of two nest predators, crows and brown-headed cowbirds. However, relationships among birdfeeders, nest predators, and nest survival were complex. Nest survival for robins declined with increasing number of bird feeders but only where crows were most frequently detected. For cardinals, nest survival rates showed no association with either feeder availability or predator activity. The different patterns for robins and cardinals may at least be partially explained by differences between these species in diet, nest placement and vulnerability to predators. My results suggest effects of anthropogenic foods on animals and mechanisms driving interspecific interactions in urban areas may vary across species.

For the final component of my work, I examined the extent to which nest sites in the residential matrix may offer protection from predation. Nest predation is known to be the leading cause of avian reproductive failure, and, as such, breeding birds should face strong pressure to select nest sites that are less detectable or accessible to predators. While several studies have failed to detect an association between nest site characteristics and nest success, what constitutes a safe nesting site likely varies across species and contexts. Therefore, I developed a series of competing models to test how vegetation characteristics of nest sites and features typical of urban areas (i.e. roads, buildings, and

anthropogenic foods) predicted nest survival for robins and cardinals breeding in yards during April-August 2011-2014. I found that nest site characteristics failed to predict nest survival for cardinals, and height was the only significant predictor of robin nest survival. I suggest that the lack of relationship between nest site characteristics and nest fate stem from a diverse predator community that effectively precludes any nest site from being predictably safe for birds breeding in the suburban matrix.

Collectively my results show that although interactions among breeding birds, their nest predators, and resources in residential yards are often complex, the suburban matrix can be managed to support conservation of certain native species. In this way, my research increases the current understanding of factors influencing the conservation value of suburban areas in order to guide wildlife management in an ever-urbanizing world. Efforts to improve the suitability of matrix habitats for native species will help conserve urban birds and complement protection of nature reserves.

For my family,

especially Joe, who keeps saying “Yes”

It’s the ride of our lives!

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Fields of Study

Major Field: Environment and Natural Resources

Specialization: Fisheries and Wildlife Sciences

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Chapter 1: Introduction

A crucial question for ecologists today is how to conserve wildlife as human populations and associated urban development continue to expand. The effects of human development on birds are particularly well-documented and indicate that urbanization can profoundly influence avian community structure and reproduction. As development intensity increases, so too does avian biomass, especially of granivorous, omnivorous, and cavity-nesting species, while species richness declines (Chace and Walsh, 2006). Yet the high abundances and densities of birds in urban areas do not necessarily reflect increased reproductive productivity in these habitats (Blair, 1996) and empirical evidence from nesting studies shows conflicting results regarding the effects of urbanization on population demography (Chamberlain et al., 2009). For instance, urban-nesting birds generally initiate laying earlier, and often have lower clutch sizes, lower nestling weights, and lower productivity per nesting attempt compared to birds that nest in undeveloped areas (Chamberlain et al., 2009), though exceptions do exist (Shustack and Rodewald, 2010).

Changes in bottom-up (e.g. vegetation and food resources) and top-down (e.g. predation) drivers in urban environments may be responsible for the observed patterns. Urbanization affects vegetation structure and floristic composition, which collectively

provide substrates for foraging, nesting and cover (Evans et al., 2009; Goldstein et al., 1986; White et al., 2005). For example, dense foliage and increased structural heterogeneity of vegetation are expected to reduce nest predation by concealing nests (Martin, 1993), but in urban areas, there may be less partitioning of nesting sites, which can facilitate the search efficiency of predators (Martin, 1988). Moreover, the prevalence of some exotic plant species promotes earlier green up of urban forests (Shustack et al., 2009), and nests in these substrates may be particularly vulnerable early in the breeding season when nest site partitioning is low because other substrates have not yet leafed out (Rodewald et al., 2010; Schmidt and Whelan, 1999). The pervasiveness of exotic vegetation in urbanizing landscapes may increase the vulnerability of nests to predation because differences in nest placement and characteristics of the nest patch may facilitate the ability of predators to locate nests in exotic substrates (Borgmann and Rodewald, 2004; Martin, 1993; Schmidt and Whelan, 1999).

Anthropogenic food resources also play a determining role in structuring avian communities and influencing population demography in urban landscapes (Robb et al., 2008a). Urban sites provide more fruits and seeds than rural areas (Leston and Rodewald, 2006) and feeders can provide a significant, though supplemental, food source (Brittingham and Temple, 1992). Supplemental food attracts birds to and increases settlement in certain areas, and is likely a key reason why densities of birds in cities are so high (Jansson et al., 1981; Shochat, 2004; Wilson, 1994). The widespread use of bird feeders in backyards may benefit avian communities by increasing overwinter survival

(Brittingham and Temple, 1988; Jansson et al., 1981) and reproductive success (Robb et al., 2008b). However, most anthropogenic food resources subsidize both breeding birds as well as their nest predators, and the effects of these supplements on predator-prey interactions remains poorly understood (Robb et al., 2008a).

Finally, shifts in predator community and predation pressure along a gradient of urbanization may significantly impact avian communities in urban landscapes. Urban areas often support a diverse predator community which has the ability to prey upon nests, fledglings, and adult birds (Fischer et al., 2012; Rodewald and Kearns, 2011). In areas where there is great diversity of nest predators and variety in predators' habitat requirements, nesting birds may be forced to co-occur with some nest predators when they place nest sites to avoid other predators (Marzluff et al., 2007). Thus, the presence of a diverse predator community may prohibit "safe" nesting sites, making the ability to re-nest quickly following predation more adaptive than nest site selection or defense (Filliater et al., 1994). However, an increase in predator abundance does not necessarily translate to increased predation pressure in urban areas. To the contrary, a relaxation of predation pressure in urban areas has been widely reported (Blair, 2004; Chamberlain et al., 2009; Gering and Blair, 1999). Studies comparing predator abundance or activity with identities of predators responsible for nest failure have shown that the most common predators may not be responsible for the majority of depredations in urban areas (Chiron and Julliard, 2007; Rodewald et al., 2011; Weidinger, 2009). This disconnect may result because anthropogenic food resources that attract predators to urban areas also help to

sustain predators when predators rely upon anthropogenic resource subsidies instead of natural prey, such as birds and their nests (Friesen et al., 2013; Rodewald et al., 2011).

However, the understanding of relationships among vegetation, food, predation and avian communities in urban areas is incomplete for several reasons. First, most research to date has employed a coarse-grain approach, examining the effects of urbanization on birds in different habitat types that represent increasing anthropogenic disturbance (Blair, 2001; Clergeau et al., 2001; Gering and Blair, 1999; Mason, 2006), or in undeveloped habitat fragments near developed areas (Marzluff et al., 2007; Rodewald and Bakermans, 2006; Thorington and Bowman, 2003). Second, although researchers have begun to examine the influence of the landscape matrix on birds in urbanizing systems (Friesen et al., 1995; Marzluff et al., 2007; Rodewald and Bakermans, 2006), few have investigated how the observed patterns are influenced by matrix characteristics specifically associated with urbanization or by the juxtaposition of developed and undeveloped habitats (Kalinowski and Johnson, 2010). Research designed to address the patterns of response to urbanization on avian populations in the developed matrix and adjacent remnant habitat simultaneously is rare (Catterall et al., 2010). Finally, comparatively few studies of avian populations in developed areas are conducted on private land (i.e. residential yards) with a study design that explores the consequences of yard management practices (Daniels and Kirkpatrick, 2006; Ryder et al., 2010).

Dissertation format

My research addresses these knowledge gaps and seeks to inform wildlife management decisions in the context of rapid urbanization by investigating how characteristics of the suburban matrix influence avian population demography. In chapter 2, I examine to what extent demographic processes operating in nature reserves and adjacent matrix habitats are linked, specifically comparing daily nest survival rates and nest predator identity between these two habitats. In chapter 3, I investigate associations between woody cover and nest predator activity in order to determine if planting trees and shrubs might have the unintended consequence of promoting activity of nest predators. In chapter 4, I use experimental and observational approaches to address how bird feeders affect relationships between breeding birds and their nest predators. In chapter 5, I assess the ability of nest site characteristics to predict nest survival rates, and test whether anthropogenic foods influence the effects of nest site characteristics on nest survival.

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Chapter 2: Urban sparing or sharing? Implications for breeding birds

Abstract

As human populations and associated research needs expand at a rapid rate, a crucial concern for ecologists is what strategy should be used to conserve biodiversity in human-dominated ecosystems such as urban landscapes. Some ecologists are proponents of protecting areas from human development and using unprotected areas intensively (land sparing), while others attest that biodiversity conservation is more effective where lands are used less intensively to meet both human and ecological objectives (land sharing). Most of debate about the utility of each of these approaches has focused on comparing species abundance or presence, with few addressing mechanisms that may influence patterns, like demographic differences. Here I evaluate differences in avian reproductive success in land-spared nature reserves (forest parks) and land-shared matrix habitats (residential yards), specifically testing the assumption that predation of avian nests is higher in matrix habitats. During April-August 2007-2014, I monitored nests of two native birds, American robin (*Turdus migratorius*) and northern cardinal (*Cardinalis cardinalis*), and video-documented nest predators in paired reserve-matrix habitats in the Columbus, Ohio metropolitan area. I found similar rates of nest survival between the two habitats for both robins (X^2_1 =0.715, p = 0.398, n= 741 nests) and cardinals (X^2_1 =0.926, p

=0.336, n= 1156 nests) but clear differences in which species were responsible for depredation events. In particular, domestic cats (*Felis catus*) were more than five times as likely to depredate cardinal nests in matrix habitats versus nature reserves (X^2_1= 7.52, simulated p = 0.011). These results highlight the potential for land-sharing in cities and suggest that increased focus on improving the suitability of matrix habitats for native species could positively impact biodiversity conservation in developed landscapes.

Introduction

Ecologists have long debated how to maintain biodiversity in the face of increasing human population and associated resource needs. The dominant conservation paradigm for most of the last century has been one of setting aside certain areas from human development while using unprotected areas intensively (Hansen and Rotella, 2002), also known as "land sparing" (Fischer et al., 2008; Green et al., 2005). However, the last two decades have spurred growing interest in an alternate mechanism for biodiversity conservation, "land sharing," where land is used less intensively with the intent to meet multiple human and ecological objectives (Fischer et al., 2008; Flynn et al., 2009). In contrast to land sparing, which focuses on efficiency through homogeneity and has its conceptual foundations in an island biogeographic model (MacArthur and Wilson, 1967), land sharing emphasizes resilience, ecosystem interactions and heterogeneity (Fischer et al., 2008).

Rising interest in land sharing and the associated land sparing vs. land sharing debate have been prompted to some extent by growing recognition of the importance of the matrix surrounding nature reserves. In contrast to island ecosystems for which the ocean matrix is uniformly inhospitable for terrestrial organisms (MacArthur and Wilson, 1967), matrix permeability and suitability are species-specific in most terrestrial systems (Prugh et al., 2008). For some species, the matrix can even provide alternate habitat to areas protected from human development (Franklin and Lindenmayer, 2009; Kupfer et al., 2006). Indeed, a growing body of research has demonstrated that matrix characteristics influence species persistence and community composition within adjacent nature reserves (Butsic et al., 2012; Hansen and Rotella, 2002; Kupfer et al., 2006; Mitrovich et al., 2010; Prugh et al., 2008; Rodewald, 2003), highlighting that role that the matrix may play in biodiversity conservation.

Although the land sparing vs. land sharing debate has focused almost exclusively on agroecosystems (Fischer et al., 2008), the same ideas can also be applied to urbanizing landscapes (Butsic et al., 2012; Lin and Fuller, 2013; Stott et al., 2015; Sushinsky et al., 2013). For example, is biodiversity within urbanizing landscapes better maintained with low-density residential development on large parcels that leave few dedicated green spaces, or with high-density development on small lots interspersed with more and larger green spaces (Pejchar et al., 2007; Sushinsky et al., 2013)? Historically, protecting natural habitat remnants from development was regarded as the primary vehicle for conservation in urban areas, with little attention paid to the more developed matrix

surrounding those nature reserves. Although sparing large green spaces in urban environments may benefit species less tolerant to urbanization (Sushinsky et al., 2013), recent research suggests biodiversity may not be well conserved within urban parks or reserves due to the influence from the surrounding city (Butsic et al., 2012; Mitrovich et al., 2010). For example, although native ant diversity was high within a regional network of nature reserves in California, reserves within 200m of urban land were more likely to be invaded by an exotic ant species and invaded reserves exhibited a 60% decline in median species richness (Mitrovich et al., 2010). If development of the matrix continues as planned, the area of protected reserves vulnerable to invasion will increase from 24% to 44% (Mitrovich et al., 2010). In addition, the decline of semi-natural habitats outside of nature reserves, some of which serve as population source areas for certain species, suggests that conservation strategies need to consider matrix habitats instead of relying solely on nature reserves to preserve biodiversity (Hansen and Rotella, 2002). Amid growing desire to employ the urban matrix to better sustain biodiversity (Gaston et al., 2005; MacGregor-Fors and Schondube, 2011), several organizations now encourage managing backyard habitats for a variety of species, especially birds and butterflies (e.g. National Wildlife Federation, nwf.org; Audubon Society, audubon.org).

Most empirical research evaluating the relative value of land-sparing versus land-sharing has compared species abundance or presence (e.g. Gagné and Fahrig, 2010; Hodgson et al., 2010; Niell et al., 2007), with far fewer considering demographic mechanisms that may influence these patterns (e.g. Hansen et al., 2005; Hansen and

Rotella, 2002). Within urban landscapes, the perception persists that animals occupying developed areas will perform worse than those in nature reserves (Hansen et al., 2005). Residential neighborhoods, in particular, are often assumed to be population sinks for urban birds because birds may experience reduced survival and reproduction near homes, often due to high predation (Thomas et al., 2012; van Heezik et al., 2010; Vierling, 2000). Likewise, housing density may be positively associated with nest predation risk and/or nest parasitism, leading to low nest success for certain species in developed areas (Hansen and Rotella, 2002; Tewksbury et al., 1998; Vierling, 2000). Loss of native vegetation due to residential development could also increase nest predation risk for birds breeding in yards, either by reducing nest site partitioning (Martin, 1995) or via increases in exotic vegetation cover (Rodewald et al., 2010; Schmidt and Whelan, 1999). In addition, there is growing concern regarding ecological impacts of synanthropic or introduced predator species on bird conservation (Baker et al., 2008; Bonnington et al., 2013; Morgan et al., 2011; Salo et al., 2007; Vierling, 2000). Domestic cats (*Felis catus*) in particular are important predators of urban birds (Balogh et al., 2011; Calver et al., 2011; Loss et al., 2013; Stracey, 2011; Thomas et al., 2012) and may be more likely to depredate birds in matrix habitats than in nature reserves in some cases (Kays and DeWan, 2004; van Heezik et al., 2010; but see Barratt, 1997).

I compared avian nest survival and predator identities in forested urban lands spared from human development (nature reserves) versus nest survival to land within the shared residential matrix. Because I used replicated pairs of sites in the matrix and

reserve, my study offers a unique opportunity to investigate if differences in nest survival between matrix and nature reserves were associated with changes in which species most frequently depredate nests. Previous research has indicated that urbanization may affect the proportion of avian versus mammalian predators (Rodewald and Kearns, 2011) especially risk of predation by cats (Stracey, 2011) and brown-headed cowbirds, *Molothrus ater* (Chace et al., 2003; Hansen and Rotella, 2002).

Methods

Data collection

I conducted this study in seven pairs of forest parks and residential neighborhoods located in the greater metropolitan area of Columbus, Ohio. These forest parks were selected for a research program initiated in 2001 to investigate the effects of urbanization on breeding birds (Rodewald and Bakermans, 2006; Rodewald and Shustack, 2008). In 2011, this research was expanded to include birds breeding in residential neighborhoods bordering seven of the most urban forest parks. I focused my research within 3-5 ha sites within forest parks and adjacent residential neighborhoods. With resident permission and along with trained technicians, I worked in 150 private yards in 2011, 173 in 2012, 151 in 2013, and 135 in 2014 (11- 32 yards per neighborhood; >50% area of each neighborhood).

I used systematic searching and behavioral observations to find nests of American robin (*Turdus migratorius,* robin) and northern cardinal (*Cardinalis cardinalis*, cardinal).

These species are the most common open-cup nesting birds in the understory and midstory of both forest parks and residential yards, however these species differ in several characteristics such as body size, diet and migratory strategy (Halkin and Linville, 1999; Vanderhoff et al., 2014). Nests were checked every 1-4 d by either directly examining nest contents or by observing parental behavior from >10m from the nest to determine the nest stage (e.g. nest building, incubation, nestlings). To avoid exposing nests to predators as a result of my visits, I varied my routes to nests, checked contents briefly, and delayed checking nests if nest predators were observed in the vicinity.

I deployed time-lapse video systems at a subset of nests in order to document which species were responsible for depredation events. Video systems were placed at cardinal nests in forest parks during 2007-2010 and at cardinal and robin nests in yards during 2011-2014. All cameras were placed at nests that allowed attachment of the camera to a nearby substrate and could be securely and discreetly deployed (i.e. to reduce chance of disturbance and theft). The willingness of residents to grant permission for video recording on their property also influenced camera placement in yards. Video systems consisted of a miniature infrared camera and time-lapse recorder in a weatherproof case (see Rodewald and Kearns, 2011 for additional details). Although using cameras to monitor nests has the potential to have an effect on the likelihood of depredation (Richardson et al., 2009), I used cameras to identify the species actually responsible for depredation events, not to estimate predation risk (c.f. Thompson and Burhans 2003; Reidy, Stake and Thompson 2008). Furthermore, I do not expect that use

of cameras affected nest survival estimates because I used cameras at only a small subset (<3%) of the total number of nests I monitored.

Statistical analysis

I used a logistic exposure model to estimate daily nest survival rates of 741 robin nests (n_{forest} = 190; n_{yard}= 551) and 1156 cardinal nests (n_{forest}= 719; n_{yard} = 437) monitored during April-August 2011-2014 using a custom 'nestsurvival' package in R (R Core Development Team, M. Herzog, *pers. comm.*). The logistic exposure model is a generalized linear model that uses a binomial error distribution and a link function that estimates probability of nest survival between each visit to the nest, thereby eliminating potential bias due to different exposure periods (Shaffer and Burger, 2004). Nest fate at each nest check was modeled as either failing (0) or surviving (1) the nest-check interval for a single null model by site, land use (matrix or reserve), year, and species. I excluded nests whose failure was confirmed to be unrelated to predators (e.g., weather; <1% of failed nests), and nests abandoned during building or where I did not confirm that a clutch was laid prior to nest failure (17%).

I used a mixed-model framework to evaluate if nest survival differed between nature reserve and residential matrix. Robins and cardinals were tested separately and models included the following parameters: year (fixed effect), land use (fixed effect) and site (random effect). I only included daily nest survival rates for sites where I had

monitored at least five nests in that year and land use. I compared models either without year or without land use (i.e. a reduced model) to the full model using a likelihood ratio test to determine the significance of year and land use (Zuur et al., 2009) and accepted alpha= 0.05 as significant.

I investigated potential differences in the proportion of depredations attributed to specific predators for cardinal nests in residential matrix versus nature reserves using a chi-squared (X^2) statistic. I specifically tested if there were differences between residential matrix and nature reserves in the proportion of avian vs. mammalian predation (Rodewald and Kearns, 2011), the proportion of cat vs. all other predation (Stracey, 2011), and the proportion of brown-headed cowbird vs. all other predation (Chace et al., 2003; Hansen and Rotella, 2002). I calculated simulated *p*-values using Monte Carlo tests with 2000 replicates because limited sample size may have influenced accuracy of exact *p*-values (Hope, 1968), and accepted alpha=0.05 as significant.

Results

Daily survival of robin nests was similar between residential matrix and nature reserve habitats (X^2_1 =0.715, p = 0.398) and among years (X^2_1 =5.382, p = 0.150), averaging 0.937 ± 0.003 (SE) across all nests monitored (Fig. 2.1; Table A.1). Daily nest survival did not differ between land uses for cardinals (X^2_1 =0.926, p =0.336) but varied among years (X^2_1 =8.064, p =0.045), with the lowest survival in 2012 (mean ± SE = 0.920

± 0.006) and the highest in 2013 (0.940 ± 0.005; Fig 2.1; Table A.2).

I identified predators at 87 depredation events at the 247 nests with video cameras (Tables A.3, A.4). I documented 6 additional depredations in yards as I was checking nests (for cardinals, one case each of depredations by cat, brown-headed cowbird and gray squirrel, *Scurius carolinensis*; for robins, three cases of depredations by American crow, *Corvus brachyrhynchos*). I documented a total of 17 distinct nest predators (Table 2.1), and cumulative number of predator species identified depredating nests in both forest and yards rose quickly with sample size (Fig. 2.2). Compared to cardinal nests in forests, depredations at cardinal nests in yards were disproportionately more attributed to cats (X^2_1= 7.52, simulated p = 0.011), but there were similar proportions of mammalian and avian predators in matrix and reserve habitats (X^2_1 = 3.13, simulated p = 0.100). The proportion of cardinal nests depredated by brown-headed cowbirds was also similar between land uses (X^2_1= 0.249, simulated p = 0.769).

Discussion

Although the relative value of land-sharing versus land-sparing approaches have been evaluated for a variety of working landscapes (e.g. agriculture, agroforestry), few have extended this idea to cities – perhaps because existing literature often points to urbanization as a primary driver of species extinctions and biodiversity loss (Czech et al., 2000; McKinney, 2006), with cities providing little conservation value (Stott et al.,

2015). Yet there is a strong need to identify the best strategies to maintain biodiversity in urbanizing landscapes, especially as human populations and developments continue to expand (Lin and Fuller, 2013; McKinney, 2002; Stott et al., 2015; Sushinsky et al., 2013). Contrary to the common presumption that the urban matrix provides marginal breeding habitat to birds, I show that land-sharing via residential yards did not depress nesting success compared to land-spared forest parks. Rather, nest survival rates for two native species, American robin and northern cardinal, were similar in the residential matrix versus adjacent nature reserves.

One important finding of this study is that species interactions, in this case between birds and some of their nest predators, varied at even fine spatial scales. Despite similar nest survival rates between two urban land uses, the most important predators of robins and cardinals were strikingly different. Though I documented a similar number of species depredating cardinal nests in yards (n= 11) and forests (n=14), brown-headed cowbirds were the top predator in forests (20%), while the top predator in yards was domestic cats (27%). Far fewer species were detected depredating robin eggs and nestlings in yards (n= 4), and American crows were the most common predator, accounting for 53% of depredation events. Although I had a limited sample size for depredations of robin nests (n=15), the four documented nest predators were detected within the first six depredations, providing evidence that I identified the suite of species most likely to depredate robin nests in my system.

Of the nest predators, cats were responsible for over five times as many depredation events in the matrix compared to nature reserves (27% vs. 5% of documented depredation events on cardinal nests in yards and forest parks, respectively), even though the proportion of mammalian and avian predators was similar between land uses. Empirical evidence that cats may have a disproportionate impact in yards compared to nature reserves has been mixed. For example, some studies have shown that cats spend the majority of their time yards compared to adjacent nature reserves (Kays and DeWan, 2004; van Heezik et al., 2010), while others provide evidence that cats readily penetrate natural habitats adjacent to developed areas (Guttilla and Stapp, 2010; Marks and Duncan, 2009; Wierzbowska et al., 2012). Moreover, habitat use and proclivity to enter natural habitats may vary among individual cats even within the same study (e.g. Barratt, 1997). One reason cat impacts may be limited in less-developed habitats in certain landscapes is because other predators, such as coyotes (*Canis latrans*), either deter or consume cats that venture into these habitats (Gehrt et al., 2013). As part of a complementary camera trap study in this system, several detections of coyotes were recorded in some of the forest parks (*L. Kearns, unpublished data*), while coyotes were never detected by camera traps placed in yards (*unpublished data*).

Independent of cat movement patterns and habitat use, several studies have documented greater hunting activity of cats in developed habitats versus less-developed ones. In one study in Albany, New York, 80% of the observed hunts occurred in yards or within 10m of the forest edge (Kays and DeWan, 2004). In another study in Gainesville,

Florida, cats were responsible for over 70% of documented depredations on northern mockingbird (*Mimus polyglottos*) nests in residential neighborhoods, but were never documented depredating mockingbird nests in parking lots, pastures, or wildlife preserves (Stracey, 2011). However, high variation in hunting activity among individual cats, including the occurrence of "super predator" cats (i.e. the few individuals who are responsible for the majority of prey returns) in certain studies, makes it difficult to predict where cats are likely to have the greatest impacts (Baker et al., 2005; Barratt, 1998; Churcher and Lawton, 1987; Kauhala et al., 2015; Loyd et al., 2013; Thomas et al., 2012; Tschanz et al., 2010).

Although the similar rates of nest survival despite hugely different rates of cat predation might initially suggest that nest predation by cats in compensatory in my system, there are important caveats. First, addressing the question of compensatory versus additive predation would require comparing mortality rates with or without (or with fewer and more) cats within the same habitat type because there may be differences in baseline nest mortality among different urban habitats. My study compared two different land uses and it is possible that the residential matrix without cats would have had much higher levels of nest survival than the residential matrix with cats, irrespective of the nest survival rates in the forest parks. Second, evaluating the population-level consequences of cat predation on avian communities would require additional demographic information across the nesting season (e.g. number of young fledged, post-fledging survival) or avian life cycle, which is why the question of cat predation being

additive or compensatory is so difficult to answer (Baker et al., 2008, 2005; Barratt, 1998; Beckerman et al., 2007; Nelson et al., 2005; Tschanz et al., 2010). Acting on the precautionary principle (Calver et al., 2011) and given that this study and others have shown a variety of direct and indirect impacts of free-ranging cats on avian reproduction (e.g. Balogh et al., 2011; Bonnington et al., 2013; Thomas et al., 2012), keeping cats indoors during the nesting season remains good practice for those wishing to minimize potential impacts of cats on urban birds.

Although the majority of biodiversity research has focused historically on habitats with low human use (Miller and Hobbs, 2002), or protected from development (Fernandez-Juricic and Jokimaki, 2001), my findings suggest that improving the quality of the developed matrix may yield positive conservation outcomes. Future research should identify the full suite of circumstances under which native species experience similar benefits in the developed matrix as in nature reserves. While others have recommended strategies for improving the conservation value of protected areas within cities (Fernandez-Juricic and Jokimaki, 2001; Pejchar et al., 2007), I suggest that recommendations should be extended into the developed matrix as well. Improving the suitability of matrix habitats for native species not only improves the suitability of the landscape as a whole (Franklin and Lindenmayer, 2009; Kupfer et al., 2006; Prugh et al., 2008), but it also provides greater ability to maintain at least some wildlife populations than simply protecting habitat "islands" from human development (Burghardt et al.,

2009; Franklin and Lindenmayer, 2009).

One caveat of this study is that my results may pertain most the suite of urban-associated birds and may not be generalizable to species that are more sensitive to human development, such as the Acadian flycatcher, *Empidonax virescens* (Rodewald and Shustack, 2008). A comparison of forested parks and residential yards required, by definition, a focus on species like robins and cardinals that most commonly breed in both of these land uses. Although my focal species were each tolerant of development, the similar pattern in nest survival they exhibited is interesting given their differences in life history characteristics (e.g. diet; Halkin and Linville, 1999; Vanderhoff et al., 2014). In terms of the relevance to conservation of work focused on common species, it is important to note that many bird species facing declines in contemporary times were once common, such as rusty blackbird, *Euphagus carolensis* (Greenberg and Droege, 1999). Thus research that informs how to "keep common birds common" is an important component of conservation because these species provide the foundation for avian biodiversity and ecosystem integrity (Partners in Flight, partnersinflight.org).

Ecologists have not yet identified the best means of reducing negative effects of urbanization on biodiversity in the face of expanding human developments. Likely, the relative value of land-sharing versus land-sparing to biodiversity is likely contextual (e.g. to specific landscapes, development types, or species; Butsic et al., 2012). Even so, this study suggests that at least in some circumstances, nest success of native birds may be

equivalent between nature reserves and adjacent residential matrix habitats. Interactions between protected and unprotected areas may have significant impacts on biodiversity conservation, for example, if wildlife in unprotected areas serve as source populations for wildlife living in protected areas (Hansen and Rotella, 2002), or if matrix habitats are managed to facilitate versus impede dispersal (Prugh et al., 2008). Thus, conservation portfolios intended to maintain urban biodiversity can rightfully include a mid of spared and shared land.

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Table 2.1. Percentage of nest depredation events attributed to predator species for 90 depredation events recorded at American robin (*Turdus migratorius*) and northern cardinal (*Cardinalis cardinalis*) nests in forest parks and residential yards within the Columbus, Ohio metropolitan area during 2007-2014. *Accipiter* species were either Cooper's hawks, *A. cooperii*, or sharp-shinned hawks, *A. striatus*. Unidentified mammals depredating robin nests were either raccoon or cat.

Predator	Forest cardinal	Yard cardinal	Yard robin
American crow, *Corvus brachyrhynchos*	7%	12%	53%
Domestic cat, *Felis catus*	5%	28%	13%
Brown-headed cowbird, *Molothrus ater*	20%	15%	-
Raccoon, *Procyon lotor*	11%	4%	13%
Accipiter sp.	9%	4%	13%
Eastern gray squirrel, *Sciurus carolinensis*	5%	15%	-
Unidentified mammal	11%	-	7%
Virginia opossum, *Didelphis virginiana*	4%	8%	-
Blue jay, *Cyanocitta cristata*	4%	4%	-
Common grackle, *Quiscalus quiscala*	7%	-	-
Eastern chipmunk, *Tamius striatus*	2%	4%	-
Unidentified snake	2%	4%	-
Rat, *Rattus* sp.	-	4%	-
Gray catbird, *Dumetella carolinensis*	4%	-	-
Unidentified bird	4%	-	-
Barred owl, *Strix varia*	2%	-	-
Northern cardinal, *Cardinalis cardinalis*	2%	-	-
Unidentified squirrel	2%	-	-
N total	55	26	15

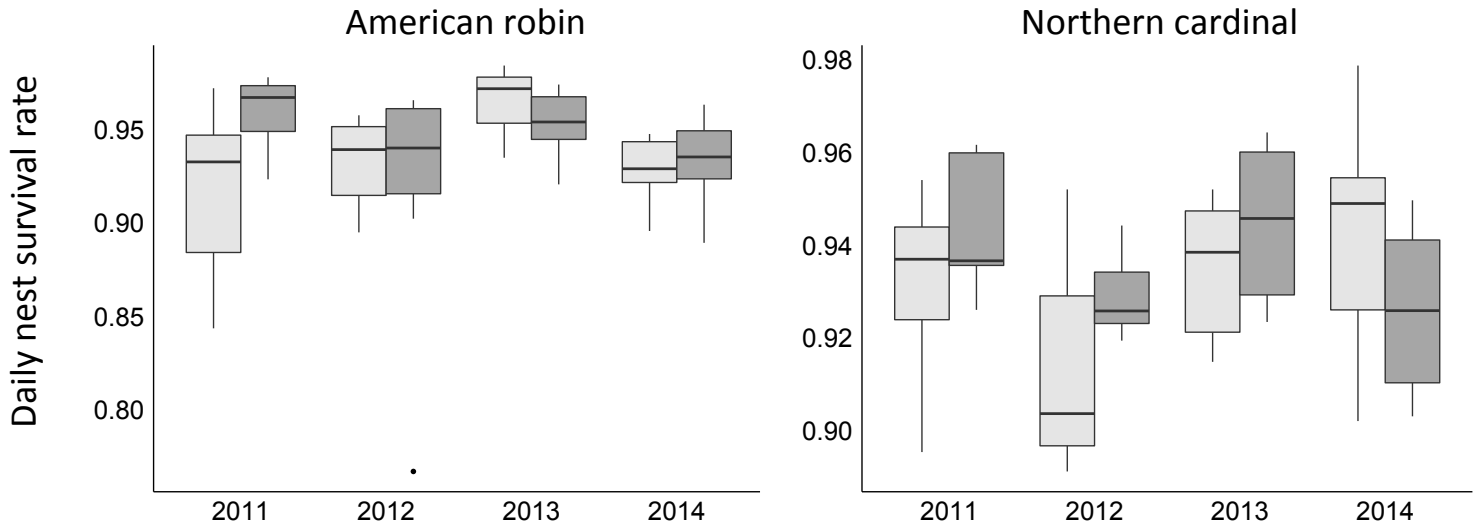

Figure 2.1. Neither American robins (X^2_1 =0.715, p = 0.398) nor northern cardinals (X^2_1 =0.926, p =0.336) experienced lower survival of nests placed in residential yards (dark gray) versus forest parks (light gray) in the Columbus, Ohio metropolitan area during 2011-2014.

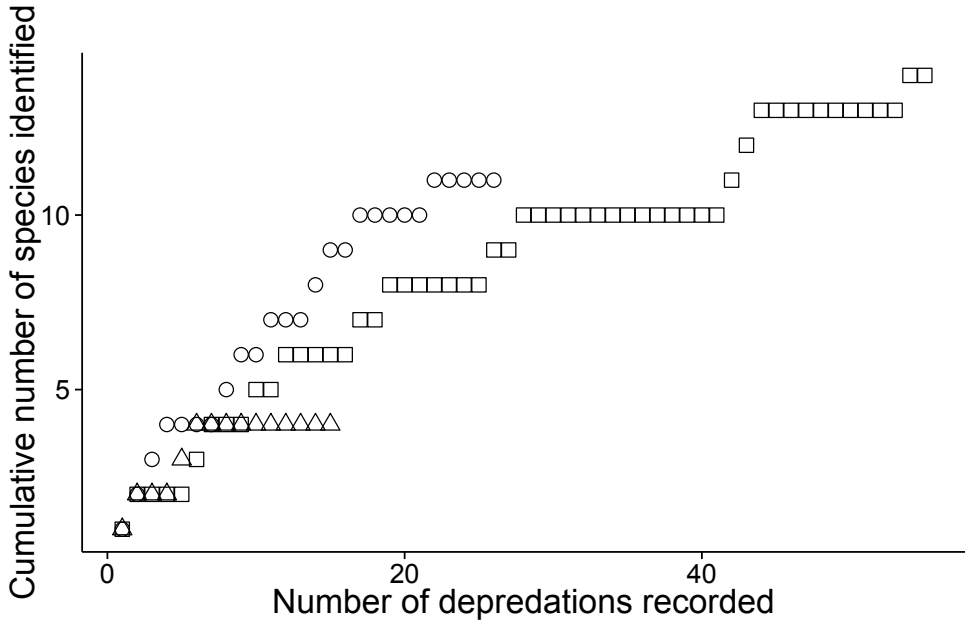

Figure 2.2. Cumulative number of nest predator species identified and sample size for 87 predation events recorded on cardinal nests in forest (squares, *n*= 55) and yards (circles, *n*= 26), and robin nests in yards (triangles, *n*= 15) in the Columbus, Ohio metropolitan area during 2007-2014.

Chapter 3: Woody cover does not promote activity of nest predators in residential yards

Abstract

Urban development often affects resource availability in ways that can influence not only community structure, but key species interactions that shape population dynamics. Although some resources are unintentionally altered, others are deliberately changed to improve habitat for urban wildlife, particularly songbirds. I hypothesized that management strategies that encourage planting trees and shrubs (i.e. increasing woody cover) would inadvertently attract predators of bird nests, which are generally abundant within cities. To test this, I examined the relationship between percent woody cover, pooled across trees and shrubs, and diurnal activity patterns of nest predators in residential yards. I surveyed predator activity and characterized habitat using aerial imagery of seven suburban neighborhoods in Franklin County, Ohio during April – August 2011 and 2012. Predator activity varied widely among individual yards, but contrary to my hypothesis, the availability of woody cover at either yard or neighborhood scales was not a strong predictor of diurnal activity in yards for five common species of nest predators (Eastern gray squirrel, *Sciurus carolinensis*; common grackle, *Quiscalus quiscala*; brown-headed cowbird, *Molothrus ater*; blue jay, *Cyanocitta cristata*; and domestic cat, *Felis catus*). Thus, this study suggests that wildlife habitat management or gardening programs that recommend increasing woody cover do not necessarily attract

some common predators of songbird nests in Midwestern landscapes. Additional research that identifies which habitat features beyond woody cover best predict nest predator activity will facilitate the creation of management recommendations that increase the conservation value of urban environments for songbirds.

Introduction

Urban green spaces can support a diverse assemblage of native biodiversity, including sensitive taxa (Bland et al., 2004; Fuller et al., 2008). Within metropolitan landscapes, residential neighborhoods in particular may be hotspots for urban biodiversity, as species richness and diversity generally peak at intermediate levels of urbanization (Blair, 2004; Clergeau et al., 2001; McKinney, 2002). To increase the suitability of yards for wildlife, wildlife-friendly gardening directs urban citizens to provide food, water, cover/shelter, and places to breed. While feeding birds has been a popular for decades (Davies et al., 2009; Lepczyk et al., 2004), more holistic approaches to conservation include supplying resources to meet a variety of needs (Gaston et al., 2007). Vegetation is often the resource of emphasis in most wildlife-friendly gardening, and programs commonly focus on strategies to reduce the amount of lawn and to increase woody cover, i.e. planting trees and shrubs, in order to provide suitable habitat for a variety of species (Gaston et al., 2005; Goddard et al., 2010; Grimm et al., 2008).

Of all of the wildlife that potentially could benefit from wildlife-friendly gardening, songbirds are often the intended recipients of habitat enhancement efforts. Providing resources to birds through feeding or other gardening practices has been popular in the US and UK for over 100 years and continues to engage millions of people

(Cooper and Smith, 2010; Cordell et al., 2008). Wildlife-friendly gardening recommendations have the potential to affect songbirds directly and indirectly. Several studies show that residents can expect positive direct effects for songbirds when implementing wildlife-friendly gardening, such as increases in abundance and species richness as food and vegetation resources increase (Daniels and Kirkpatrick, 2006; Fuller et al., 2008). However, indirect effects of wildlife-friendly gardening are less well-understood, and some of these may be negative for urban songbirds. For example, bird feeding is posited as one driver of biotic homogenization of avian assemblages in urban environments (Blair and Johnson, 2008; Chace and Walsh, 2006; Kark et al., 2007), and has the potential to facilitate disease transfer among songbirds (Bradley and Altizer, 2007; Robb et al., 2008a). In particular, there is a poor understanding of how changing resource availability as a result of wildlife-friendly gardening practices may influence species interactions, including those between songbirds and their nest predators (Robb et al., 2008a).

One potential, though often unrecognized, complication of increasing trees and shrubs in residential yards is that woody cover may attract predators of songbirds and their nests (Alterio et al., 1998; Yanes and Suarez, 1996). Woody cover provides nest predators with food resources (e.g. fruit, nuts, small mammals, songbirds and nests) and protection from predation by other species (Parker and Nilon, 2012). Increased woody cover from exotic honeysuckle (*Lonicera maackii*) in urban forest fragments is associated with decreased nest survival for songbirds due to increased nest predation (Rodewald et al., 2010) and brood parasitism (Rodewald, 2009). Vegetation buffers planted to protect hoiho (*Megadyptes antipodes*) chicks in New Zealand had the unintended consequence of

attracting nest predators, presumably in response to increased prey activity in planted buffers (Alterio et al., 1998). The possibility of trees and shrubs attracting nest predators is particularly troublesome given that nest predators often reach high densities in cities as compared to exurban areas due to use of anthropogenic foods and relaxation of top-down controls (Fischer et al., 2012; Longcore et al., 2009; Parker and Nilon, 2012; Prange et al., 2004). Thus any positive effects of woody cover for songbirds could be diminished if activity of nest predators is higher in these areas, and if exposure to predators is a primary driver of nest predation rates. However, increases in wildlife-friendly habitat and food-bearing plants were associated with an increase in the proportion of British gardens frequented by some generalist predators but not others (Baker and Harris, 2007), and more research is warranted to quantify the effects of individual habitat features on nest predator use of yards.

Complicating the understanding of associations between predators and vegetation is that the spatial scale at which nest predators respond to habitat in urban areas remains unknown. While breeding songbirds may be sensitive to habitat characteristics at fine scales (Daniels and Kirkpatrick, 2006), nest predators may select habitats at geographic scales much greater than that of residential yards. While design and management at the scale of individual yards has been shown to be useful for predicting patterns of use of certain species of birds (Daniels and Kirkpatrick, 2006) and mammals (Baker and Harris, 2007), there is debate about the appropriateness of the yard scale for informing conservation due to the potential of spatial autocorrelation of habitat features within neighborhoods (Warren et al., 2008) and the necessity of maintaining habitat at scales beyond that of individual yards in order to support viable wildlife populations (Goddard

et al., 2010; Warren et al., 2008). Gaining a better understanding of how characteristics at the scale of yards and neighborhoods influence generalist species such as nest predators will help advance discussions regarding the use of these two scales in wildlife management and conservation.

I explored how landowner decisions about vegetation management influenced predator activity at yard and neighborhood scales. I hypothesized that the structural and food resources provided by trees and shrubs would attract predators, and thus, predicted that predator activity would be positively associated with woody cover.

Methods

Study area

This study was conducted within 7 suburban neighborhoods in Franklin County, Ohio which is located within the greater metropolitan area of Columbus with >1.9 million residents (Figure A1; US Census Bureau, 2013). With resident permission and along with trained technicians, I worked in 150 private yards in 2011 and 173 private yards in 2012 (13 to 32 yards per neighborhood; >50% of area of each neighborhood). I included as many yards as possible within 3.5 ha bordering riparian forest parks used for complementary research (Rodewald and Shustack, 2008). Neighborhoods were similar in area (~3.5 ha), and variations in age, building density, and landscape composition are described in Table 3.1 (see Rodewald and Shustack, 2008 for methods).

Vegetation characteristics, including availability of woody cover, also varied greatly among neighborhoods (Fig 3.1). Vegetation in yards at Casto and Elk Run was planted <30 years ago when these subdivisions were developed, and common species

included Bradford pear (*Pyrus calleryana*), purple-leaf sand cherry (*Prunus* x *Cistena*), river birch (*Betula nigra*), boxwood (*Buxus* sp.), red maple (*Acer rubrum*), and sugar maple (*Acer saccharum*). Intact, mature vegetation dominated yards in the remaining neighborhoods and common species included apples (*Malus* sp.), oaks (*Quercus spp.*), black walnut (*Juglans nigra*), spruces (*Picea* sp.), arborvitae (*Thuja* sp.), Eastern white pine (*Pinus strobus*), silver maple (*Acer saccharinum*), sugar maple *(Acer* saccharum), burning bush (*Euonymus alatus*), privets (*Ligustrum* sp.) and exotic honeysuckles (*L. maackii, L. japonica*).

Data collection

I conducted diurnal predator surveys weekly from 16 May to 27 August 2011 and 16 April to 12 August 2012. This time period corresponds to the breeding season for several species of songbirds that nest in residential yards, including northern cardinal (*Cardinalis cardinalis*) and American robin (*Turdus migratorius*), whose nests were monitored as part of complimentary research. Surveys consisted of a ten-minute point count of unlimited distance conducted between 0700 h and 1300 h. I recorded predator species, method of detection (visual or aural) and the radial distance to each individual detected. Within each neighborhood, I randomly selected eight yards in which to conduct surveys from the properties where I had access, and centered six of the surveys ten meters from the front door of the building and two of the surveys ten meters from the back door of the building. Four of the surveys were conducted between 0700 h and 1000 h and four of the surveys were conducted between 1000 h and 1300 h to minimize potential bias of

differences in activity patterns of predators throughout the morning. Statistical analysis includes only survey locations that remained the same in 2011 and 2012; as a result, only 7 survey locations in the Elk Run were used for analysis (n_{total}= 55). Surveys were not conducted during periods of heavy rain and I completed 12 or 13 surveys per yard in 2011 and 16 or 17 surveys per yard in 2012.

I characterized habitat at two scales using satellite imagery and aerial photography recorded on 28 and 29 May 2010 available in Google Earth (Google Inc., 2013). Using ArcGIS (Environmental Research Systems Institute, 2010), I first defined buffers for my two scales and created point features to represent random locations within these buffers. I standardized the map view to 1:400 and categorized the points in respect to habitat feature they first intersected as either woody cover or other (e.g. building, lawn, road; c.f. Evans et al., 2009). Thus, if a point intersected tree canopy, it was considered woody cover even if a different habitat feature, such as a road, was present under the canopy. Each point only encompassed one type of habitat feature. The appropriate classification was apparent for a majority of points, but where imagery was ambiguous the point location was compared to ground-truthed maps of habitat features completed for all of the yards for which I had access. Use of aerial imagery to characterize habitat precluded my ability to identify plant species or to distinguish between cover from trees versus shrubs, so all woody cover was pooled into a single metric (c.f. Evans et al., 2009).

My smaller geographic scale included habitat under the management of two to five property owners, hereafter *yard scale*. To characterize habitat at the yard scale, I defined a 30-m yard buffer (0.28 ha) around each survey center and I generated twenty

random points within each of these buffers. The area included in the yard scale was identical for all neighborhoods (8 yards x 0.28 ha = 2.24 ha). My larger geographic scale included habitat within a boundary defined by drawing a convex polygon that encompassed the eight yard buffers in each neighborhood (n=7), hereafter *neighborhood scale*. Within the neighborhood buffers, I generated an additional 160 (i.e. 20 x 8) random points, and repeated the identification process. Survey locations, arrangement of roads, property sizes, and number of buildings influenced the spatial configuration of neighborhood buffers. As a result, area within the neighborhood polygons ranged from 2.6 to 4.9 ha because of the spatial arrangement of the survey centers even though the size of all of the focal neighborhoods was ~3.5 ha.

Data analyses

I defined *predator activity* as the mean number of detections for a species at a survey center. Because this metric is based on detections, differences among yards and neighborhoods are better interpreted as relative differences in diurnal activity levels or patterns of habitat selection, not as differences in predator densities (c.f. Baker and Harris, 2007; Rodewald et al., 2011). Although surveys were conducted with an unlimited radius, for analysis I only included observations within a 30-m radius of the survey center to minimize bias of detection as distance increases (Buckland et al., 2001). This area (0.28 ha) defined the yard scale and corresponded to the area included in habitat characterization of yards. Species detected >200 times total were included in analysis,

and data were pooled between years prior to analysis where paired t-tests indicated no difference ($p > 0.05$) in mean predator activity between years for a species.

I performed Mantel tests for spatial autocorrelation to determine if there were strong spatial patterns among yards within a neighborhood that could confound analysis (Mantel, 1967). Mantel tests quantify the degree of similarity between (1) a matrix of geographic distances between locations (e.g. survey centers) and (2) a matrix of differences between environmental parameters (e.g. predator activity, vegetation characteristics). I defined significant correlations as those with $p < 0.05$, indicating a strong spatial structure of the data.

I used an information-theoretic framework that compared the relative weight of evidence for multiple models with Akaike Information Criterion corrected for small sample sizes to examine the association between predator activity in yards and percent woody cover (AIC_c; Burnham and Anderson, 2002). I used percentage of points identified as woody cover within the yard buffers (hereafter, *yard woody cover*) and within the neighborhood buffers (hereafter, *neighborhood woody cover*) as predictor variables in models of predator activity. Percent woody cover stabilized once 12 out of 20 points were classified in yards. All candidate models included the interaction between neighborhood and neighborhood woody cover as a random effect to account for neighborhood-specific effects; the null model included this as its only term. I considered the model with the lowest AIC_c value the best model and competing models ($< 2\ \Delta\ AIC_c$) equally plausible. Akaike weights (w_i, weight of evidence for each model) indicated the relative support for each model and the likelihood that any given model was the true best model. Model averaging was used to derive parameter estimates for plausible models

where the null model was not within the set of plausible models. Each predator species was analyzed individually and statistics were derived from linear mixed models constructed in R (R Core Development Team, 2013).

Results

In 1635 diurnal surveys I detected 13 nest predator species (Table 3.2), all of which have been video-documented depredating songbird nests in forest parks studied in complementary research (Rodewald and Kearns, 2011). There was great variation in frequency of predator detections across species, and the five predator species detected >200 times total were included in analysis: Eastern gray squirrel (*Sciurus carolinensis*), common grackle (*Quiscalus quiscala*), brown-headed cowbird (*Molothrus ater*), blue jay (*Cyanocitta cristata*) and domestic cat (*Felis catus*). Data were pooled between years for Eastern gray squirrel, common grackle, brown-headed cowbird and blue jay, and were analyzed separately for domestic cat per results of paired t-tests. I found no strong patterns of spatial autocorrelation of predator activity within a neighborhood; significant correlations ($p<0.05$) were identified for only four neighborhood-predator species combinations (Table B.1). Five of the seven neighborhoods showed no significant spatial autocorrelation of percent woody cover among yards (Table B.2).

Both percent woody cover (Fig 3.2) and predator activity (Fig 3.3) varied within and among neighborhoods. Values for neighborhood woody cover were similar to the mean values for yard woody cover within each neighborhood (Fig 3.2), and were positively correlated, $r\,(53) = 0.63$, $p<0.01$. Contrary to my prediction, woody cover at neither yard nor neighborhood scales predicted activity for common grackle, brown-

headed cowbird, blue jay or domestic cat (Table 3.3). Although woody cover models ranked high for Eastern gray squirrel, 95% confidence intervals around the parameter estimates indicate effect sizes were small and not ecologically significant. Model averaged estimates showed that squirrel detections per survey increased by 0.02 ± 0.01 for each increase in yard woody cover, and by 0.05 ± 0.03 for each increase in neighborhood woody cover. The upper estimate for these effect sizes equate to an increase of less than two additional squirrel detections across the 12 to 17 surveys completed over the course of the season for a given yard.

Discussion

Contrary to my prediction, I found no strong relationship between woody cover at either yard or neighborhood scales and activity of five common diurnal species of nest predators in yards. The lack of association between woody cover and nest predator activity cannot be attributed to insufficient variation in either availability of woody cover across yards and neighborhoods or nest predator activity (c.f. Sims et al., 2007), or by spatial autocorrelation, which was infrequent among my sites. These findings are consistent with other studies reporting high variation in resource availability within a given neighborhood and highlight the importance of behaviors of individual residents or small groups of residents in determining resource availability in urban areas (Faeth et al., 2005; Goddard et al., 2010; Grimm et al., 2008; Shochat et al., 2006). Indeed, the idea that individual landowners can positively influence habitat suitability of yards for wildlife by changing resource availability is an underlying premise of wildlife-friendly gardening programs (Gaston et al., 2007).

I also documented high variation in predator activity patterns across species and my two geographic scales that were not unduly influenced by spatial autocorrelation. While differences in predator activity patterns among neighborhoods could be due to differences in predator densities, it is unlikely that differences in densities would drive the variation in predator activity that I documented at the yard scale (0.28 ha) within the same neighborhood (~3.5 ha). Results of this study provide further evidence of non-uniform patterns of habitat selection of potential nest predators in suburban areas (Baker and Harris, 2007; Rodewald et al., 2011).

Although this study was not designed to monitor activity of nocturnal predator species (e.g. raccoon, *Procyon lotor*; and Virginia opossum, *Didelphis virginiana*), video recordings show that most species responsible for nest depredations in this system are diurnal, and no single predator is dominant (Ch. 2; Rodewald and Kearns, 2011). The five diurnal predator species included in analysis are among the most important predators in this study system, collectively accounting for 41% of depredations in yards (Ch. 2) and 40% of depredations in adjacent forest parks (Rodewald and Kearns, 2011). In contrast, raccoon and Virginia opossum account for just 12% of depredations in yards (Ch. 2) and 14% of depredations in adjacent forest parks (Rodewald and Kearns, 2011).

I may have been unable to document a link between percent woody cover and diurnal activity of nest predators because most of the species included in analysis are generalists that are not closely associated with a particular resource by definition. In urban areas, expected associations between habitat variables such as woody cover and predators may be superseded by the availability of anthropogenic resources that these generalist species have learned to exploit (e.g. use of dumpsters as predictable food

sources and structures as nesting/denning sites; Prange and Gehrt, 2004). Cats may not be closely associated with woody cover because they have their ecological needs met via associations with humans (Sims et al., 2007).

The lack of association between woody cover and predator activity may have been an artifact of my choice of habitat metric. It was not possible to distinguish tree cover versus shrub cover or identify vegetation species because my habitat characterization relied upon aerial imagery. As such, percent woody cover does not reflect specific vegetation characteristics that may be more closely associated with individual nest predators (e.g. the importance of mast resources for squirrels; Parker and Nilon, 2012) or allow us to identify how trees versus shrubs have different influences on individual nest predators. However, percent woody cover was used because it met my objective to determine how recommendations of wildlife-friendly gardening may influence predator activity patterns, and in turn, species interactions among predators and prey. I chose to explore the effect of percent woody cover at relatively fine scales (0.28 and 3.5 ha) because these correspond to the scales at which recommendations for wildlife-friendly gardening are frequently implemented, and the scales at which individual residents have the ability to respond (i.e. individual yards or collections of yards; Goddard et al., 2010). Similarly, percent woody cover reflects the broad recommendation of wildlife-friendly gardening to add trees and shrubs, as few programs include directives of which vegetation species participants should plant beyond broad categories (e.g. native species, fruiting shrubs).

Understanding the ecological consequences of habitat alterations is needed to evaluate their effectiveness of wildlife-friendly gardening, especially for songbirds

(Gaston et al., 2005). Growing interest in bird-related recreation will likely lead to additional efforts of individuals to provide better habitat for songbirds, and management recommendations should be supported with empirical research. I found no strong evidence that increasing woody cover, a central recommendation of wildlife-friendly gardening, encouraged activity of nest predators in yards. This suggests that the exposure of songbird nests to predation may not increase with increased availability of woody cover in yards and neighborhoods. Combined with knowledge of the positive effects of woody cover for conservation of urban songbirds (Clergeau et al., 2001; Daniels and Kirkpatrick, 2006; Evans et al., 2009; Savard et al., 2000), findings of this study support planting trees and shrubs to improve yard habitats for songbirds. However, the combination of fine-scale differences in predator activity patterns within residential neighborhoods and the inability of percent woody cover to reliably predict these patterns indicates that additional research is necessary to better understand how yard characteristics beyond vegetation influence nest predators, and in turn, reproductive success of songbirds. Future research should investigate what other habitat attributes, such as availability of food resources or presence of particular plant species, may be responsible for spatial variation in activity of nest predators. Identification of these factors influencing nest predator activity is crucial for maximizing the conservation value of residential yards for breeding songbirds.

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Table 3.1. Age and landscape composition within 1-km of seven focal neighborhoods in Franklin County, Ohio. Urban index is a principal component factor that loads positively for number of buildings, percent cover by road, pavement and lawn, but negatively for percent cover by agriculture. Adapted from Rodewald and Shustack, 2008.

				Proportion			
Neighborhood	Year Built	No. of Buildings	Urban Index	Mowed	Paved	Road	Agriculture
Elk Run	1980	812	-0.16	0.27	0.06	0.05	0.31
Cherry	1930-1960	997	0.76	0.36	0.16	0.07	0.02
Woodside	1980	1227	0.32	0.4	0.07	0.05	0.11
Rush Run	1940-50	1611	0.75	0.41	0.09	0.06	0.06
Kenny	1910-1950	1733	0.89	0.34	0.17	0.06	0
Casto	2000	1776	1.25	0.42	0.20	0.08	0
Tuttle	1910-1960	2285	1.61	0.34	0.30	0.09	0

Table 3.2. Frequency at which nest predators were observed within 30 meters of 55 survey locations in residential yards in Franklin County, Ohio during 1635 diurnal surveys conducted April-August 2011 and 2012. The five species observed more than 200 times total were included in analysis.

Predator Species	2011	2012	Pooled
Eastern gray squirrel, *Sciurus carolinensis*	320	401	721
Common grackle, *Quiscalus quiscala*	213	263	476
Brown-headed cowbird, *Molothrus ater*	152	239	391
Blue jay, *Cyanocitta cristata*	88	116	204
Cat, *Felis catus*	107	95	202
American crow, *Corvus brachyrhynchos*	28	72	100
Eastern chipmunk, *Tamius striatus*	53	32	85
Cooper's hawk, *Accipiter cooperii*	8	5	13
Red squirrel, *Tamiasciurus hudsonicus*	9	2	11
Raccoon, *Procyon lotor*	1	3	4
Eastern fox squirrel, *Sciurus niger*	0	2	2
Eastern striped skunk, *Mephitis mephitis*	0	1	1
Red-shouldered hawk, *Buteo lineatus*	1	0	1
American kestrel, *Falco sparverius*	1	0	1

Table 3.3. Relative fit of models explaining variation in nest predator activity in residential yards using Aikaike's Information Criterion corrected for small sample sizes (AIC_c). Models include percent woody cover within 30 meters of survey centers (yard) and within a 100% minimum convex polygon encompassing yards in which surveys took place in each neighborhood (neighborhood). Surveys were conducted at 55 yards in seven suburban neighborhoods in the Columbus, Ohio metropolitan area in 2011 and 2012. Data were pooled between years unless indicated. *K*, number of parameters; ΔAICc, distance from top model; w_i, model weight.

Predator Species	Model	K	AICc	ΔAICc	w_i
Eastern gray squirrel	Yard + Neighborhood	5	44.01	0	0.29
	Yard*Neighborhood	6	44.47	0.46	0.23
	Yard	4	44.53	0.52	0.23
	Neighborhood	4	44.81	0.8	0.2
	Null	3	47.49	3.48	0.05
Common grackle	Yard*Neighborhood	6	9.76	0	0.32
	Null	3	9.9	0.14	0.3
	Neighborhood	4	11.12	1.36	0.16
	Yard	4	11.49	1.72	0.13
	Yard + Neighborhood	5	12.21	2.45	0.09
Brown-headed cowbird	Null	3	-23.98	0	0.52
	Yard	4	-22.21	1.77	0.22
	Neighborhood	4	-21.65	2.33	0.16
	Yard + Neighborhood	5	-19.84	4.13	0.07
	Yard*Neighborhood	6	-18.15	5.83	0.03
Blue jay	Null	3	-56.47	0	0.35
	Neighborhood	4	-56	0.46	0.28
	Yard	4	-55.07	1.4	0.18
	Yard*Neighborhood	6	-54	2.47	0.1
	Yard + Neighborhood	5	-53.62	2.84	0.09

continued

Table 3.3, continued

Domestic cat, 2011	Null	3	13.37	0	0.54
	Yard	4	15.36	1.98	0.2
	Neighborhood	4	15.63	2.26	0.17
	Yard + Neighborhood	5	17.76	4.39	0.06
	Yard*Neighborhood	6	19.53	6.16	0.02
Domestic cat, 2012	Null	3	-44.85	0	0.51
	Yard	4	-42.81	2.04	0.18
	Neighborhood	4	-42.66	2.19	0.17
	Yard + Neighborhood	5	-41.27	3.58	0.09
	Yard*Neighborhood	6	-40.36	4.49	0.05

Figure 3.1. Mean percent woody cover ranges from 10% (Casto, left) to 61% (Cherry, right) across the seven neighborhoods in the Columbus, OH metropolitan area included in analysis. Aerial images recorded 28 May 2010; available from Google Earth.

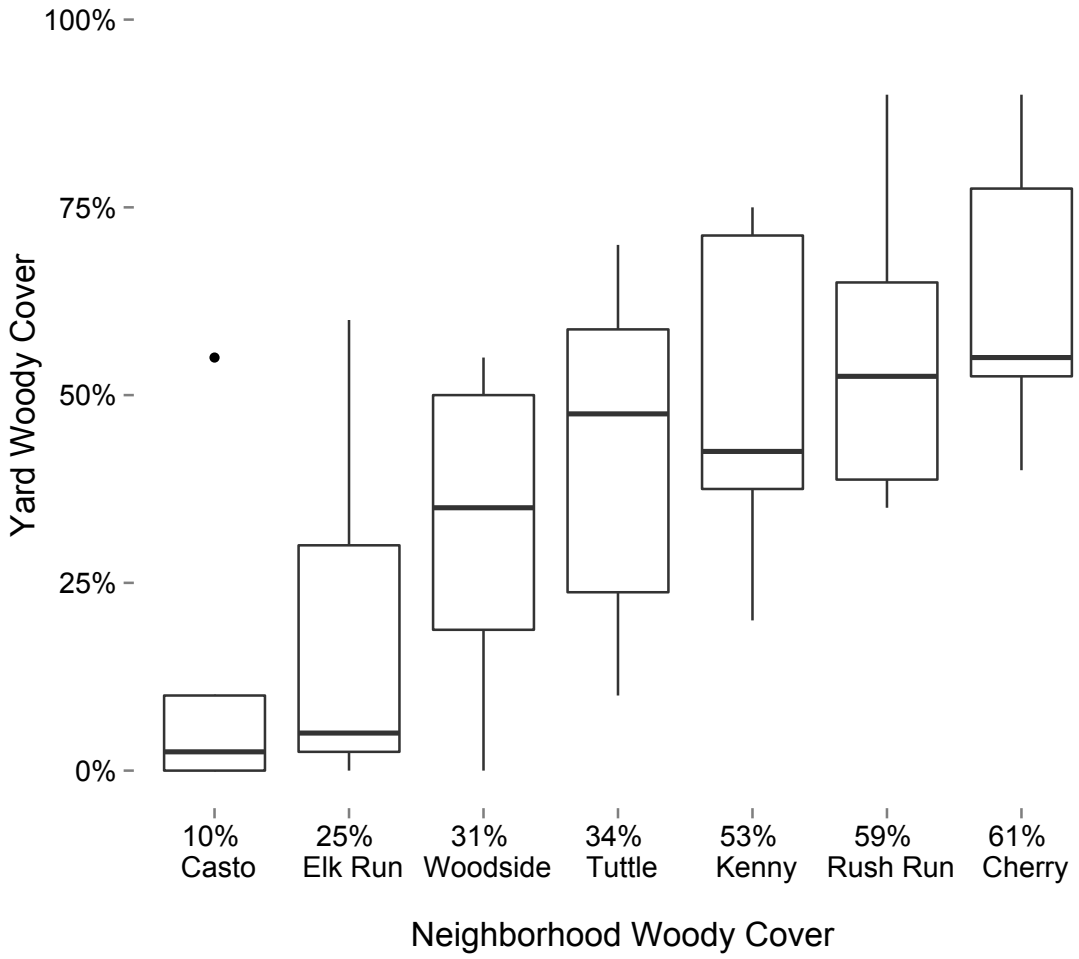

Figure 3.2. Variation in yard woody cover among 55 yards within seven suburban neighborhoods in the Columbus, Ohio metropolitan area. Values for neighborhood woody cover are indicated above neighborhood name on the x-axis.

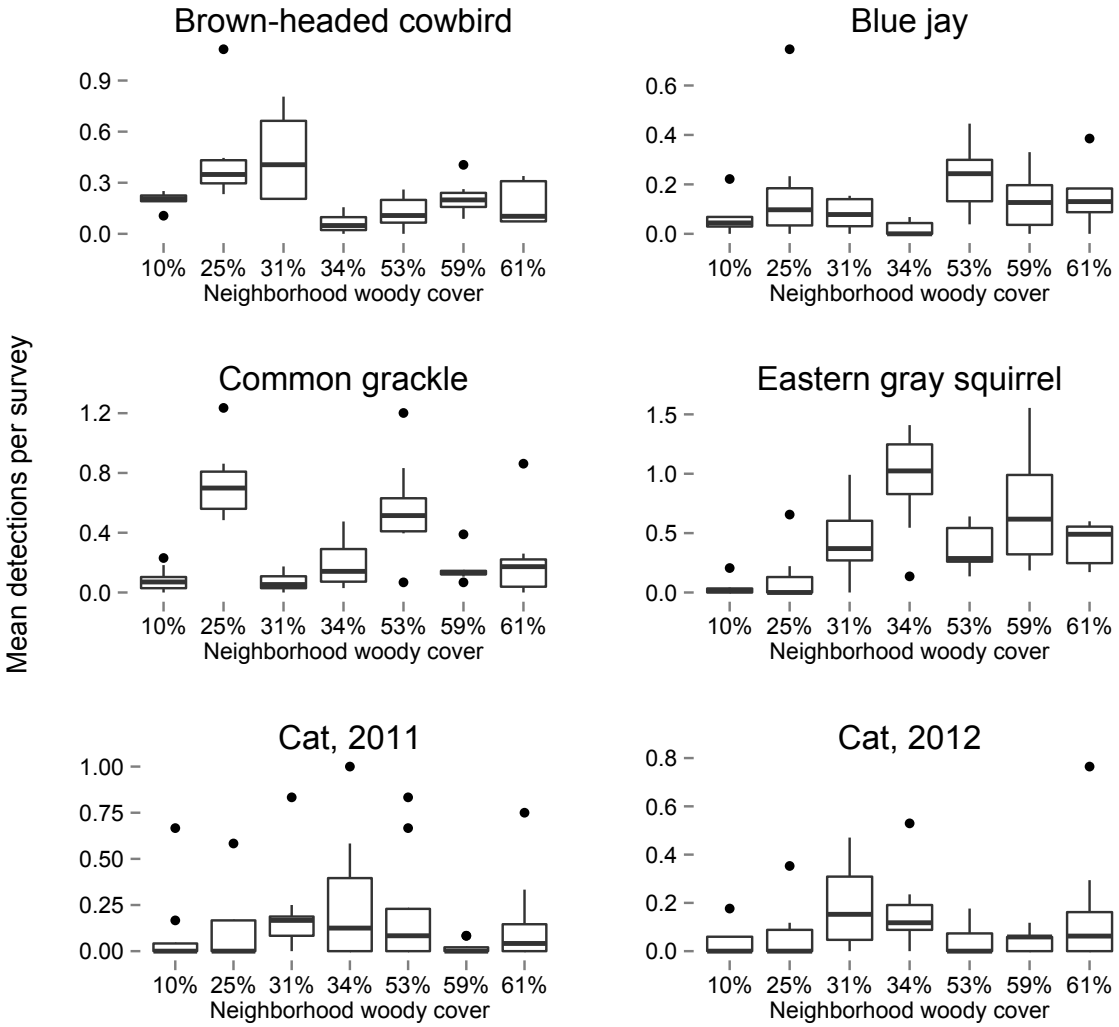

Figure 3.3. Variation in mean number of detections per survey for five predator species in seven suburban neighborhoods of Columbus, Ohio 2011-2012. Data are pooled between years except where indicated.

Chapter 4: Species-dependent effects of anthropogenic foods on predators and prey

Abstract

Anthropogenic food subsidies can profoundly shape the environment that an animal experiences, but the consequences for species interactions remain poorly understood. I used observational and experimental approaches to investigate how subsidies (i.e. bird feeders) affected predator-prey dynamics in neighborhoods of the Columbus, Ohio, USA metropolitan area. From April-August 2011-2014, I quantified bird feeders, diurnal activity of six common nest predators and nest survival of two songbirds. Effects of anthropogenic subsidies varied among predator and prey species. Bird feeders were positively associated with diurnal activity of two nest predators, American crow (*Corvus brachyrhynchos*) and brown-headed cowbird (*Molothrus ater*). The relationship among food, predators, and nest survival was complex. Nest survival for American robins (*Turdus migratorius*) declined with increasing number of bird feeders but only where crows were most frequently detected. In contrast, nest survival rates of northern cardinal (*Cardinalis cardinalis*) were not related to either feeder availability or diurnal predator activity. Differences between robins and cardinals in diet, nest placement and vulnerability to predators may partially explain the different patterns I detected. Results of this study suggest effects of anthropogenic foods on animals and mechanisms driving interspecific interactions in urban areas may vary across species.

Introduction

Resource subsidies, particularly in the form of food, can strongly shape animal communities through their effects on behavior, population dynamics, and species interactions. Within species, access to resource subsidies can change movement patterns (Beckmann and Berger, 2003; Eide et al., 2004; Longcore et al., 2009; Prange et al., 2004) and enhance population productivity (Arcese and Smith, 1988; Polis et al., 1997; Rastogi et al., 2006). Among species, food subsidies can alter interactions to the extent that community composition shifts (Boutin, 1990; Brown and Munger, 1985; Prange and Gehrt, 2004). In addition, food subsidies may influence predation risk, for example, risk might be greater in areas near subsidies (Borgmann et al., 2013; Newsome et al., 2015; Preston and Rotenberry, 2006). Alternately, subsidies may reduce predation pressure on certain natural prey (Takimoto et al., 2002), either when predators directly consume subsidies (Dahle et al., 1998) or when subsidies are associated with changes in predator diets to different prey species (Newsome et al., 2014).

Urban areas provide an excellent opportunity to examine how subsidies may influence predator-prey dynamics because abundant and diverse supplemental foods are a defining characteristics of cities (Warren et al., 2006). Anthropogenic subsidies provided through both intentional (e.g. bird feeders; Robb et al., 2008a) and unintentional means (e.g. poor refuse management; Beckmann and Berger 2003; Bozek *et al.* 2007) often make patchy resources more continuously available in space and time (Shochat et al., 2006). Interactions between breeding birds and their nest predators may be especially influenced by anthropogenic foods because both songbirds (Robb et al., 2008a) and generalist predators readily exploit these resources (e.g. corvids, Marzluff *et al.* 2001;

squirrels, Parker and Nilon 2008; mesopredators, Prange and Gehrt 2004; Theimer *et al.* 2015) - thus congregating in the same areas. However, despite many studies on avian reproduction in urban landscapes, no clear pattern has emerged regarding the effect of urbanization and associated foods on nest survival (see Chamberlain et al., 2009 for a review). Current understanding is limited because field experiments that supplement predators are infrequent (Borgmann et al., 2013; Preston and Rotenberry, 2006; Theimer et al., 2015).

Anthropogenic subsidies can affect nest predation risk in different ways depending upon the underlying mechanisms. Subsidies may relax predation pressure because predators switch to anthropogenic foods and depredate nests less frequently (*Predator Subsidy Consumption Hypothesis*; Fischer et al., 2012). Alternately, effects of prey switching may be offset if subsidies attract predators to the area and lead to greater rates of incidental nest predation (Schmidt et al., 2001); resulting in no net change in predation rate (*Incidental Predation Hypothesis*; Stracey, 2011). Anthropogenic foods might also attract but fail to satiate potential predators, which then depredate bird nests, thereby reducing nest survival for birds breeding in areas with anthropogenic foods (*Hyperpredation Hypothesis*; Borgmann et al., 2013).

I combined observational and experimental approaches to evaluate the relative support for each subsidy hypothesis, focusing on two urban-adapted bird species and six common nest predators (Table 4.1). Under the *Predator Subsidy Consumption Hypothesis*, I expected nest survival to increase with the availability of anthropogenic foods. The *Incidental Predation Hypothesis* would be supported if there was no apparent

association between food availability and nest survival despite a positive association between anthropogenic food and predator activity. Finally, a decline in nest survival with increasing food availability and predator activity would support the *Hyperpredation Hypothesis*.

Methods

Field methods

Study area

This research was conducted in seven residential neighborhoods (~ 3.5 ha) in the greater metropolitan area of Columbus, Ohio. I selected neighborhoods that were adjacent to riparian forest parks being used for complementary long-term research (Rodewald and Shustack, 2008). Neighborhoods had similar ranges of building density and landscape composition (see Rodewald and Shustack, 2008). With resident permission and along with trained technicians, I worked in 150 private yards in 2011, 173 in 2012, 151 in 2013, and 135 in 2014 (11- 32 yards per neighborhood; >50% area of each neighborhood).

Nest monitoring

I monitored nests of American robin (*Turdus migratorius,* robin) and northern cardinal (*Cardinalis cardinalis*, cardinal) because these are most common open-cup nesting birds in the understory and midstory of residential yards within focal neighborhoods. Also, these species may respond differently to supplemental food because

1) unlike cardinals, robins rarely consume birdseed (Halkin and Linville, 1999; Vanderhoff et al., 2014) and 2) the frequency at which individual predator species depredate nests differs between robins and cardinals (Ch. 2). Nests were checked every 1-4 d by either directly examining nest contents or by observing parental behavior from >10m from the nest to determine the nest stage (e.g. nest building, incubation, nestlings). To avoid exposing nests to predators as a result of my visits, I varied my routes to nests, checked contents briefly, and delayed checking nests if nest predators were observed in the vicinity. After the nest had fledged or failed, I used an ocular tube held 1m from the nest in each of six directions (four cardinal directions, above, and below) to estimate the percent of the nest that was concealed by vegetation or other obstruction (e.g. part of a building for a robin nest on a drainpipe). For some nests it was not possible to obtain these measurements because the nest was destroyed during a depredation event or because the nest was located in a yard where I did not have permission to access.

Diurnal predator surveys

I conducted diurnal surveys of potential predators weekly from 16 May to 27 August 2011, 16 April to 12 August 2012, 22 April to 10 August in 2013, and 21 April to 7 August in 2014. Surveys consisted of a 10-min point count of unlimited radius conducted between 0700 h and 1300 h, during which I used aural and visual cues to detect a wide variety of small mammals, raptors, corvids, and mesopredators known to be nest predators in this study system (Rodewald and Kearns, 2011). Observers were trained in distance estimation and provided with rangefinders (Buckland et al., 2001). I recorded

predator species, method of detection (visual, aural, or both), the distance to each individual detected, and method of distance measurement (rangefinders or visual estimate).

Within each neighborhood, I randomly selected eight yards in which to conduct surveys from the pool of yards where I had access. I centered six surveys 10 m from the front door of the building and two surveys 10 m from the back door of the building (n_{total} = 56). In most cases the survey center was in an open part of the yard; while this meant observers visible to potential nest predators, it also insured that there was high detection probability at the survey center (Buckland et al., 2001). The same survey locations were used throughout the study with the exception of nine surveys that were moved because permission changed among years; these were relocated to the next nearest yard where I had access. Of the eight surveys, half were conducted during 0700 -1000 h and half during 1000 - 1300 h to minimize potential bias of differences in activity patterns of predators throughout the morning. Surveys were not conducted during periods of heavy rain.

Food surveys

I surveyed each neighborhood monthly between April and August 2011-2014 to determine the locations and extent of anthropogenic foods. Surveys across all seven neighborhoods were conducted within the same 7-d period of the month. I created aerial

maps for focal neighborhoods using GIS data of parcel boundaries, roads, and buildings from the Ohio Geographically Referenced Information Program (http://ogrip.oit.ohio.gov/). Trained observers spent 35-55 min per survey walking the neighborhood and identifying the locations of anthropogenic foods on these maps. Observers entered all properties where I had access for nest monitoring, and visually inspected remaining properties from a distance (i.e. on public property). Every effort was made to survey the extent of the neighborhood included in nest monitoring studies, but because I were not able to survey every yard due to access restrictions or visual obstruction (e.g. a privacy fence), these results represent conservative estimates of anthropogenic food resources in these neighborhoods. For each food source detected, I recorded food type (i.e. type of birdseed, pet food, trash, or compost) and whether or not it was accessible to avian and/or mammalian nest predators. Hummingbird feeders were considered unavailable to nest predators, as were thistle-specific feeders, provided there was no seed under the feeder. I recorded each food item separately, including where there were multiple foods present at a single location (e.g. several bird feeders hanging from the same pole), which occurred for ~40% of foods.

Experimental supplementation

To test how supplemental foods influenced predator-prey interactions, I experimentally supplemented three of the seven neighborhoods by providing a consistent quantity and quality of birdseed. I chose to manipulate birdseed because birdseed 1) represented 82% of all anthropogenic food resources available to potential nest predators

in this system, 2) was consumed by most species that I video-documented depredating nests (Ch. 2), and 3) was deliberately provided by residents, unlike other anthropogenic food resources (e.g. trash).

For the supplementation experiment I selected three neighborhoods with the fewest feeders and no permanent sources of trash (dumpsters) in 2011-2012. During April- August 2013 and 2014, I provided 13-16 feeders to each supplemented neighborhood ($n_{total} = 45$) to increase the number of feeders to 20-25, which reflects the greatest number of bird feeders observed across all neighborhoods in 2011-2012 (Table 4.2). Experimental feeders were designed to be accessible to songbirds and generalist nest predators and consisted of a shallow platform mounted on a 1.2m pole or hung from a tree. Feeders were located within sight of one or more predator survey locations, to enhance my ability to detect changes in diurnal predator activity as a function of feeder availability, and/or in proximity to areas where I had documented robins or cardinals nesting in 2011 and 2012, to enhance my ability to identify whether supplemental food increased or decreased nest survival rates. Because multiple feeders often occurred in individual yards (43% in 2011 and 63% in 2012), most experimental feeders (84%) were placed in pairs on the same pole or tree. The same locations were used for supplemental feeders during 2013 and 2014, except in two instances where residents requested that I move or remove feeders because residents were concerned that the feeders attracted undesirable wildlife.

Spatial and temporal heterogeneity in the availability of bird feeders is common in urban environments (Davies et al., 2009), and the supplementation experiment provided a

predictable, but not continuous, alternate food resource. I provided 9 kg (0.45-1.36 kg seed/feeder) of high-quality birdseed to each supplemented neighborhood once weekly. The seed blend consisted of 30% white millet, 30% milo, 22% black oil sunflower, 10.5% safflower, and 2.5% peanuts (>9% protein, >11% fat, <15% fiber). This seed blend was used because it was comparable to the most common mix detected on food surveys in 2011 and 2012 (used at 35% and 30% of all available feeders, respectively). I filled experimental feeders only once per week (i.e. I did not provide supplemental food *ad libitum*) and most experimental feeders were depleted within seven days. Monthly food surveys (see "Food surveys" above) were conducted three or four days after filling the feeders.

Statistical analysis

Predator activity

I modeled detection probability for predator species for which I had at least 450 diurnal detections after removing the 5% most distant observations (Buckland et al., 2001) using the 'distance' package in R 3.0.1 (R Core Development Team, 2013), and only these species were included in subsequent analyses. These models account for differences in detection probability associated with increasing distance between observers and nest predators, and allow for comparison of relative differences in activity among surveys (Buckland et al., 2001). Half-normal, uniform and hazard rate key functions with the option of cosine series expansions are robust models for point survey data, but each of these may not fit the data equally well (Buckland et al., 2001). As such, I used an

information-theoretic framework that compared the relative weight of evidence among these models with Akaike Information Criterion (AIC) to identify the most appropriate model to use to account for detection probability (Burnham and Anderson, 2002). I used the best-fitting model according to AIC values to calculate a diurnal activity index for each species, year, month and neighborhood. My survey method did not allow us estimate abundance because I could not identify individual predators, therefore differences in activity index among yards and neighborhoods were interpreted as relative differences in diurnal activity (c.f. Baker and Harris 2007; Rodewald, Kearns, and Shustack 2011).

Feeders and predator activity

I used linear mixed models to examine the relationship between bird feeder availability and diurnal predator activity, running separate models for each predator species. Monthly activity index was used as a response variable, and predictors were the number of bird feeders available in that month, year (fixed effect) and neighborhood (random effect). I calculated *p*-values based on student's *t*-distributions and accepted alpha =0.05 as significant.

Predator activity, feeders, and nest survival

I used the logistic exposure model to estimate the daily nest survival rate (DSR) of 521 robin nests and 428 cardinal nests monitored during April-August 2011-2014 (Fig.

C.1). The logistic exposure model is a generalized linear model that uses a binomial error distribution and a link function that estimates probability of nest survival between each visit to the nest, thereby eliminating potential bias due to different exposure periods (Shaffer and Burger, 2004). Nest fate at each nest check was modeled as either failing (0) or surviving (1) the nest-check interval. I excluded nests whose failure was confirmed to be unrelated to predators (e.g., weather; <1% of failed nests), and nests abandoned during building or where I did not confirm that a clutch was laid prior to nest failure (17%). I also excluded nests for which one or more nest checks were missing associated predator activity data (see predator activity results below).

I compared the relative weight of evidence for multiple mixed-effects models with AIC corrected for small sample sizes (AIC_c; Burnham and Anderson 2002) to assess the ability of feeder and predator metrics to explain variation in predicted DSR, testing robins and cardinals separately. Nest predators in this study system were identified using video recordings at nests as part of a complementary study (Ch. 2), and only known nest predators were included in analyses. Global models included feeders and diurnal activity indices as main effects, as well as interaction terms for feeders and activity indices for the predators that consume birdseed. A feeder × cat interaction was not considered because cats do not use birdseed as an alternative food source, and although cats may hunt birds and small mammals around bird feeders, feeders may not expose birds to higher predation risk (Dunn and Tessaglia, 1994; Woods et al., 2003). All models included neighborhood (random effect), year (fixed effect) and day of year of the nest check (fixed effect) because previous work in this study system shows that nest survival increases as the breeding season progresses (Rodewald and Shustack, 2008).

I centered and scaled feeder and diurnal predator activity indices 1) to minimize likelihood of model non-convergence due to variables on vastly different scales and 2) to enhance interpretability of interaction terms (Schielzeth, 2010). I specified a global model and then generated a candidate model set which included the global model and all subordinate models (Grueber et al., 2011). Models with interaction terms always also included those main effects. I considered the model with the lowest AIC_c value the best model and competing models ($<2\ \Delta\ AIC_c$) equally plausible. Akaike weights (w_i, weight of evidence for each model) indicated the relative support for each model and the likelihood that any given model was the true best model of the candidate model set (Burnham and Anderson, 2002). I calculated parameter estimates from natural averages of parameters included models for which $\Delta\ AIC_c < 2$ and used these to predict values for DSR.

Experimental supplementation

Effects on predator activity. I used linear mixed models to examine the effect of supplementation on diurnal predator activity as defined by detection probability models, testing each predator species separately. Models included the following fixed effects: year, treatment (experimental or control) and year × treatment; as well as the random effect of year within neighborhood to account for my repeated-measures design. I used log-likelihood ratio tests to identify the most appropriate variance structure and modeled variance as different across years, treatments, or year × treatment where there was heteroscedascity in diurnal predator activity (Zuur et al., 2009).

Effects on nest survival. I used the logistic exposure model to estimate DSR for each species, year and neighborhood using a custom R package ('nestsurvival,' M. Herzog, *pers. comm.*) using 521 robin nests and 428 cardinal nests monitored during April-August 2011-2014. The resulting DSR estimates for robins and cardinals were used as the response variable in separate linear mixed models to examine the effect of supplementation on DSR. Predictor variables included the fixed effects of year, treatment (experimental or control) and year × treatment; and the random effect of year within neighborhood to account for my repeated-measures design. I excluded DSRs from neighborhoods where I monitored fewer than 5 nests in one or more years.

Results

Predator activity

I completed 778 surveys in 2011, 945 in 2012, 868 in 2013, and 880 in 2014. In total I recorded 15,115 diurnal detections of 19 nest predator species: brown-headed cowbird (*Molothrus ater*, *n*=3376), common grackle (*Quiscalus quiscala*, *n*=3282), blue jay (*Cyanocitta cristata*, *n*=3258), eastern gray squirrel (*Sciurus carolinensis*, *n*=2340), American crow (*Corvus brachyrhynchos*, *n*=1776), domestic cat (*Felis catus*, *n*=526), eastern chipmunk (*Tamius striatus*, *n*=217), Cooper's hawk (*Accipiter cooperii*, *n*=108), red-tailed hawk (*Buteo jamaicensis*, *n*=81), red-shouldered hawk (*Buteo lineatus*, *n*=41), red squirrel (*Tamiasciurus hudsonicus*, *n*=30), raccoon (*Procyon lotor*, *n*=14), sharp-

shinned hawk (*Accipiter striatus*, *n*=9), eastern fox squirrel (*Sciurus niger*, *n*=8), American kestrel (*Falco sparverius*, *n*=3), black rat snake (*Pantherophis obsoletus*, *n*=1), broad-winged hawk (*Buteo platypterus*, *n*=1), common rat (*Rattus norvegicus*, *n*=1) and eastern striped skunk (*Mephitis mephitis*, *n*=1). Nearly all detected species were also video-documented depredating songbird nests in this study (Ch. 2) or adjacent forest parks (Rodewald and Kearns, 2011), though the most frequently-detected species were not those most often documented depredating nests in this system (Appendix A).

I modeled detection probability and calculated activity indices for the six species for which I had over 450 diurnal detections after removing the 5% most distant observations: brown-headed cowbird (cowbird), common grackle, blue jay, eastern gray squirrel (squirrel), American crow (crow), and cat. I used the model with the lowest AIC value to calculate estimates for predator activity for each combination of species, year, month and neighborhood, except in 9 instances where visual inspection of plots indicated an overfit of the model to the data and resulting activity indices were 8-10 x greater than maximum number of individuals detected in a single survey. For these cases I instead used the model with the second lowest AIC value to calculate estimates for diurnal predator activity. I lacked predator activity data from April 2011 because surveys started in May of that year. I also lacked sufficient diurnal detections across my focal neighborhoods to accurately model detection probability for brown-headed cowbirds in August 2013 or for cats in August 2014; values for activity of these species in these months were considered NA in further analyses.

Feeders and predator activity

The availability of bird feeders differed across years and among neighborhoods (Table 4.2). The extent to which bird feeders predicted diurnal predator activity varied among species (Fig. 4.1). Activity of cowbirds was positively associated with feeders (mean ± SE =0.192 ± 0.055; t_{125}=3.482, p<0.001) and varied among years, with activity in 2013 higher than in other years (t_{125}=4.445, p< 0.001). Activity of crows was also positively associated with feeders (0.026 ±0.007; t_{132}=3.896, p<0.001). Feeders were not significantly related to activity of squirrels (0.080 ± 0.073; t_{132}=1.084, p>0.05), blue jays (0.016 ± 0.012; t_{132}=1.315, p>0.05), cats (-0.058 ± 0.066; t_{125}=-0.887, p>0.05) nor common grackles (-0.019 ± 0.061; t_{132}=-0.314, p>0.05).

Predator activity, feeders, and nest survival

The following predictor variables were used to model DSR of robins: feeder availability, crow activity, cat activity, and the interaction of feeder availability and crow activity (i.e. feeder × crow). Of the 10 candidate models for robins, the feeder × crow model (crow + feeder + feeder × crow) best predicted DSR and no other models were within Δ AIC_c < 2 (Table 4.3). The top model had 60% of the total weight and predicted robin DSR as: DSR = 3.41 - 2.28(crow) – 0.368(feeders) – 0.581(crow × feeders) + 0.751(day of year of nest check) – 0.378($year_{2012}$) – 0.160($year_{2013}$) – 0.578($year_{2014}$); using $year_{2011}$ as a reference category. Feeder availability and diurnal crow activity interacted such that nest survival was especially low for robins nesting in neighborhoods with many feeders and high crow activity (Fig. 4.2).

I used the following predictor variables when modeling cardinal DSR: feeder availability, avian activity (summed across all avian predators prior to rescaling), cat activity, squirrel activity, the interaction of feeder availability and avian activity, and the interaction of feeder availability and squirrel activity. I combined all birds into a single activity index because avian predators rely on similar (i.e. visual) cues to detect nests (Söderström et al., 1998) and to maintain a lower ratio of number of predictor variables compared to sample size (Grueber et al., 2011). Eleven of the 26 candidate models for cardinal DSR, including the null model, were considered plausible (Table 4.4). Effect sizes for feeder and predator parameters were small and confidence intervals for each of these overlapped zero after model-averaging the parameter estimates (Table 4.5).

Experimental supplementation

Diurnal predator activity was highly variable among years and treatments (Fig. 4.3). However, I did not observe an increase in mean activity for any predator species in response to supplementation after accounting for differences in variance across years (squirrel, blue jay), or years and treatments (cowbird, cat, common grackle). Mean diurnal activity decreased across the study period for squirrels (mean ± SE = -1.134 ± 0.515, t_{15} =-2.200, p= 0.040), and crows (-0.118 ± 0.050, t_{19} =-2.375, p= 0.028) independent of treatment, while activity within a species was comparable across years and treatments for remaining species. In addition, DSR estimates were similar among years and between treatments for both cardinals (n=422 nests) and robins (n=551 nests; Fig. 4.4).

Discussion

I found evidence for two hypotheses explaining how anthropogenic foods may affect predator-prey interactions in urban environments- the *Hyperpredation Hypothesis* (Borgmann et al., 2013) and *Incidental Predation Hypothesis* (Stracey, 2011). Certain predators, American crows and brown-headed cowbirds, were more active in areas with bird feeders. However, food availability interacted with diurnal predator activity, such that robins only experienced depressed nest survival in neighborhoods with many feeders and high crow activity, supporting the *Hyperpredation Hypothesis*. In contrast, the lack of association between nest survival of cardinals and either feeders or diurnal predator activity was consistent with the *Incidental Predation Hypothesis*. Anthropogenic foods may have different effects on predator-prey interactions in urban areas depending on the extent to which subsidies attract and satiate predators. Taken together, results of this study demonstrate that effects of anthropogenic foods on predator-prey dynamics in urban areas are complex and may be species dependent.

Although most nest predators in this study system readily consumed birdseed, diurnal detections of only two of six predators examined were positively related to bird feeders, and no predator species increased activity in response to experimental supplementation. The high levels of spatial and temporal variability in diurnal predator activity are likely at least partially responsible for the lack of a strong response of most predators to bird feeders. Another contributing factor may have been the diverse diets of the omnivorous predators in this study system, which should make these species less

reliant upon any single food item compared to carnivores or other specialists (e.g. Cooper's hawks, Estes and Mannan, 2003). The likelihood of a generalist omnivore becoming more specialized is further reduced where the anthropogenic subsidy is variable itself. Although bird feeders are common in urban areas (Robb et al., 2008a), they may be intermittently filled and the majority of feeders may be empty at any given time (Davies et al., 2009).

Nest survival of robins declined with increasing bird feeders only where crows were most active, which suggests that bird feeders attracted and supplemented crows but did not replace robin nest contents as a food source. Crows were the most frequent predator of robin nests in this study system, with 53% of documented depredations attributed to this species (Ch. 2). Crows exist at high densities and experience high reproductive success in suburbs (Marzluff et al., 2001; McGowan, 2001), but even though adults may exploit anthropogenic foods, these subsidies are nutritionally inadequate for normal young development (Pierotti and Annett, 2001). As with many birds, crow diets change seasonally and are dominated by animal protein rather than plant matter (Verbeek and Caffrey, 2002) and natural versus anthropogenic foods (Kristan and Boarman, 2003) during periods when nestlings are being provisioned. In contrast, species that lactate to meet nutritional needs of young may be more flexible in dietary requirements (e.g. able to rely on anthropogenic resources to meet the energetic needs of self and young), as might be the case with raccoons, the other main predator of robins in this study system, raccoons (Ch. 2). Although I did not document a response of robin nest survival to experimental supplementation, these subsidies may not have had a marked

effect on nest survival of robins if supplemented neighborhoods also had low crow activity during supplementation.

Differences in vulnerability to predators, diet, and nest placement may explain why nests survival of cardinals was unrelated to either subsidies or diurnal predator activity and showed no response to experimental supplementation. First, the diversity of species that depredate cardinal nests (n=10 for cardinals versus n=4 for robins; Ch. 2) makes it unlikely that any one species, even if it responded positively to the presence of feeders, would drive changes in nest survival rates for cardinals. Indeed, no individual species was responsible for >30% of depredations on cardinal nests in this study system (Ch. 2; Rodewald and Kearns, 2011). In addition, most (>70%) documented depredations on cardinal nests were attributed species (i.e. mammals and cowbirds) that do not need to switch to natural foods during the breeding season to support growing young, as do crows. Second, bird feeders may have buffered risk of nest predation for cardinals because adult cardinals directly consume birdseed (Halkin and Linville, 1999), unlike adult robins (Vanderhoff et al., 2014). Access to supplemental food may reduce nest predation risk for cardinals by minimizing time spent foraging (Komdeur and Kats, 1999; Rastogi et al., 2006) or the number of on/off bouts (Lima, 2009; Martin, 1992). Third, the relatively greater concealment of cardinal versus robin nests may make cardinal nests less vulnerable to incidental nest predation, which occurs when secondary prey are opportunistically consumed by generalist predators searching for primary prey (Vickery et al., 1992). Post-hoc analysis showed cardinal nests were more concealed than robin nests both above (mean cover = 88% vs. 72%; $F_{1, 745}$=8.150, p=0.036) and to the sides (73% vs. 64%; $F_{1, 745}$=7.279, p=0.043). Moreover, cardinal nests may be less detectable

to predators because cardinals seldom used manmade structures as nest substrates, unlike robins, for which 15% of nests were placed on structures.

There are several limitations to my study design that could be addressed in future research in order to better understand how supplemental food affects predator-prey dynamics. I am unable to determine if the increased activity for crows and cowbirds associated with bird feeders reflected changes in predator abundance or increased activity of individuals because I were not able to identify individual predators on diurnal surveys. In addition, because the survey protocol did not allow us to detect differences in predator abundance during this study, there may have been numerical changes in predators that were not reflected in activity indices. Future studies should be designed to allow comparisons of predator abundance and/or densities, for example through use of mark-recapture of predators.

My use of diurnal surveys likely limited my ability to sample the full suite of species known to depredate robin and cardinal nests in my system (Ch. 2; Rodewald and Kearns, 2011). For example, activity of some of the species known to depredate nests is better measured at other times of day (e.g. at night for species like raccoons and opossums). However, by examining the suite of six predators that I did collectively accounts for the majority of depredations on both robin and cardinal nests (74% and 66%, respectively; Ch.2). In addition, although I had sufficient detections to estimate diurnal cat activity, future research should also consider nocturnal cat activity because of differences in cat movement patterns throughout the diel cycle (Barratt, 1997; Metsers et al., 2010; Thomas et al., 2014; but see van Heezik et al., 2010; Horn et al., 2011) and

because avian nests may be more vulnerable to cat predation at night (Appendix A, Stracey, 2011).

Finally, the positive association of crows and cowbirds with feeders across this study system despite no apparent increase in activity when supplemented together suggest that anthropogenic resources over a longer time period may be necessary to provoke measureable changes in activity, perhaps via numerical responses of populations to subsidies. Experiments in which free-ranging predators are subsidized are relatively rare (Borgmann et al., 2013; Preston and Rotenberry, 2006; Theimer et al., 2015) but have a great potential to identify mechanisms by which species interactions are influenced by resource subsidies.

This study shows that responses of predators and prey to food subsidies were complex and context dependent, even given that most of the species considered were known to consume anthropogenic foods. Species-specific responses to food subsidies may partially explain lack of a consistent pattern among studies of nest survival in the face of urbanization and increasing amounts of anthropogenic foods (Chamberlain et al., 2009). In addition, while others have shown anthropogenic subsidies may dampen fluctuations in resource availability in urban areas (Shochat et al., 2006), results in this study provide evidence that food availability, nest predator activity, and nest survival may show tremendous inter- and intra-annual variation. In this way, my work highlights how human-dominated environments are highly variable systems and thus may not amendable to simple generalizations about the effects of supplemental foods on nest survival.

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Table 4.1. Predictions under three alternate hypotheses of how anthropogenic food resources may influence diurnal nest predator activity and nest survival.

Hypothesis	Prediction
Predator Subsidy Consumption	No relationship between diurnal predator activity and nest survival
	Food availability positively related to nest survival
	Supplementation enhances nest survival
Incidental Predation	No relationship between food availability and nest survival
	Food availability positively related to diurnal predator activity
	Supplementation increases diurnal predator activity
Hyperpredation	Food availability negatively related to nest survival
	Food availability positively related to diurnal predator activity
	Supplementation depresses nest survival

Table 4.2. Minimum, maximum, and mean number of bird feeders accessible to nest predators in control and experimental neighborhoods during April-August 2011-2014. Experimental neighborhoods were supplemented with 20 lb of birdseed weekly across 13-16 feeders during April-August.

			Feeder availability		
Neighborhood	Year	Treatment	Min	Max	Mean
Casto	2011	Control	0	2	1.2
	2012	Control	1	5	2.2
	2013	Control	1	5	2.6
	2014	Control	0	5	2.4
Kenny	2011	Control	9	20	13.8
	2012	Control	6	21	14.4
	2013	Control	7	20	12.4
	2014	Control	3	16	8.4
Rush Run	2011	Control	9	15	12.0
	2012	Control	11	21	16.0
	2013	Control	11	14	12.6
	2014	Control	6	12	8.0
Tuttle	2011	Control	0	3	1.8
	2012	Control	0	3	1.8
	2013	Control	0	4	1.2
	2014	Control	0	1	0.4
Cherry	2011	Pre-supplemented	4	9	7.2
	2012	Pre-supplemented	5	13	8.8
	2013	Supplemented	12	28	19.4
	2014	Supplemented	8	15	12.6

continued

Table 4.2, continued

Elk Run	2011	Pre-supplemented	0	6	4.4
	2012	Pre-supplemented	2	9	6.2
	2013	Supplemented	10	20	14.0
	2014	Supplemented	3	9	6.8
Woodside	2011	Pre-supplemented	2	6	4.8
	2012	Pre-supplemented	4	6	4.8
	2013	Supplemented	18	25	21.4
	2014	Supplemented	6	21	16.0

Table 4.3. Model selection for robin daily nest survival rates, ranked using Akaike's Information Criterion corrected for small sample sizes (AIC_c), with models used to generate parameter estimates indicated in bold. Models with interaction terms included those main effects, and all 10 candidate models also included year (fixed effect, *n*=4), day of year of the nest check (fixed effect) and neighborhood (random effect). *k*= number of parameters, LL=logLikelihood, Δ AIC_c = distance from top model, w_i = Akaike weight.

Model	df	LL	AIC_c	Δ AIC_c	w_i
Crow × Feeder	**9**	**-1185.11**	**2388.27**	**0**	**0.60**
Cat + Crow × Feeder	10	-1185.11	2390.29	2.01	0.22
Crow + Feeder	8	-1188.06	2392.17	3.90	0.09
Cat + Crow + Feeder	9	-1187.99	2394.03	5.76	0.03
Feeder	7	-1190.53	2395.11	6.83	0.02
Crow	7	-1190.82	2395.67	7.40	0.01
Crow + Cat	8	-1190.28	2396.61	8.33	0.01
Cat + Feeder	8	-1190.44	2396.93	8.66	0.01
Null	6	-1192.94	2397.91	9.64	0
Cat	7	-1192.25	2398.53	10.26	0

Table 4.4. Model selection for cardinal daily nest survival rates, ranked using Akaike's Information Criterion corrected for small sample sizes (AIC_c), with models used to generate parameter estimates indicated in bold. Models with interaction terms included those main effects, and all 26 candidate models also included year (fixed effect, *n*=4), day of year of the nest check (fixed effect) and neighborhood (random effect). *k*= number of parameters LL=logLikelihood, Δ AIC_c = distance from top model, w_i = Akaike weight.

Model	df	LL	AIC_c	Δ AICc	w_i
Squirrel	**7**	**-972.33**	**1958.72**	**0**	**0.10**
Cat + Squirrel	**8**	**-971.49**	**1959.04**	**0.32**	**0.09**
Squirrel × Feeder	**9**	**-970.5**	**1959.09**	**0.37**	**0.09**
Cat	**7**	**-972.75**	**1959.55**	**0.83**	**0.07**
Cat + Squirrel × Feeder	**10**	**-969.78**	**1959.67**	**0.94**	**0.07**
Null	**6**	**-973.93**	**1959.89**	**1.17**	**0.06**
Avian + Squirrel	**8**	**-971.93**	**1959.93**	**1.21**	**0.06**
Avian	**7**	**-973.05**	**1960.16**	**1.43**	**0.05**
Avian + Cat	**8**	**-972.08**	**1960.23**	**1.5**	**0.05**
Avian + Cat + Squirrel	**9**	**-971.16**	**1960.4**	**1.68**	**0.05**
Squirrel + Feeder	**8**	**-972.24**	**1960.55**	**1.82**	**0.04**
Avian + Squirrel × Feeder	10	-970.37	1960.84	2.12	0.04
Cat + Feeder + Squirrel	9	-971.41	1960.91	2.18	0.04
Cat + Feeder	8	-972.69	1961.44	2.72	0.03
Cat + Avian + Squirrel × Feeder	11	-969.68	1961.48	2.76	0.03
Feeder	7	-973.83	1961.71	2.99	0.02
Avian + Feeder + Squirrel	9	-971.89	1961.88	3.15	0.02
Avian + Feeder	8	-973.04	1962.16	3.43	0.02
Avian + Cat + Feeder	9	-972.07	1962.24	3.51	0.02
Avian + Cat + Feeder + Squirrel	10	-971.13	1962.37	3.65	0.02

continued

Table 4.4, continued

Squirrel × Feeder + Avian × Feeder	11	-970.37	1962.86	4.14	0.01
Cat + Squirrel × Feeder + Avian × Feeder	12	-969.68	1963.51	4.78	0.01
Squirrel + Avian × Feeder	10	-971.75	1963.6	4.88	0.01
Avian × Feeder	9	-972.86	1963.8	5.07	0.01
Cat + Avian × Feeder	10	-971.88	1963.86	5.14	0.01
Cat + Squirrel + Avian × Feeder	11	-970.99	1964.1	5.38	0.01

Table 4.5. Parameter estimates for the effect of feeders and predator activity on cardinal daily nest survival rates averaged across eight plausible models. RI= relative importance.

Parameter	Estimate	SE	*z*	*P*(>|*z*|)	95% CI	RI
(Intercept)	2.742	0.163	16.797	<0.001	(2.422, 3.061)	
DOY	0.510	0.116	4.386	<0.001	(0.282, 0.738)	1.00
2012*	-0.170	0.177	0.961	0.3367	(-0.518, 0.177)	0.25
2013	0.112	0.188	0.595	0.5518	(-0.256, 0.479)	"
2014	-0.196	0.169	1.162	0.2451	(-0.527, 0.135)	"
Squirrel	-0.221	0.147	1.502	0.133	(-0.510, 0.067)	0.68
Cat	-0.177	0.133	1.331	0.183	(-0.438, 0.084)	0.44
Avian	0.179	0.178	1.008	0.313	(-0.169, 0.528)	0.28
Feeder	0.137	0.169	0.807	0.419	(-0.195, 0.468)	0.27
Feeder × Squirrel	-0.416	0.221	1.877	0.061	(-0.849, 0.018)	0.21

*2011 used as reference category

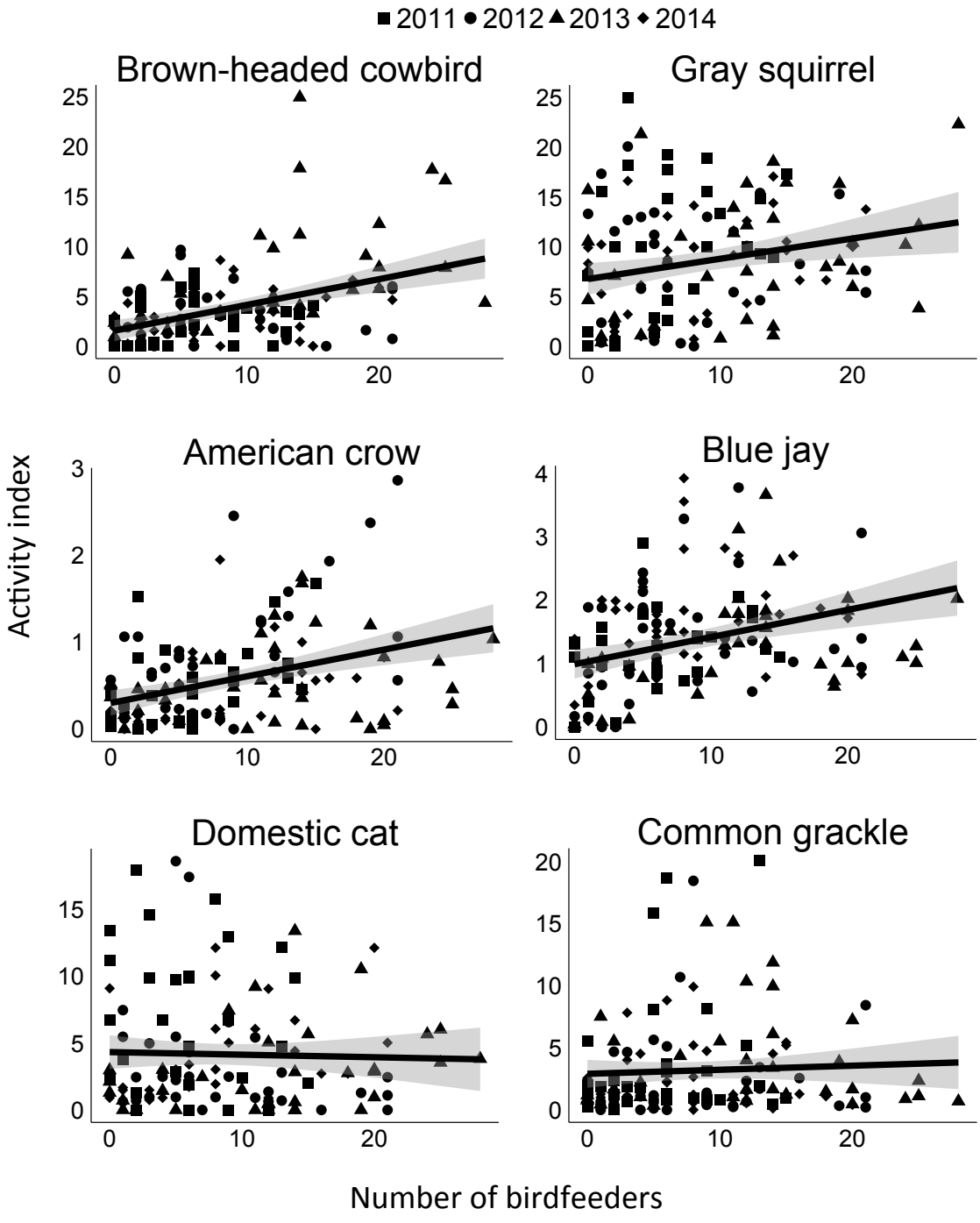

Figure 4.1. The relationship between bird feeder availability and activity was either positive or neutral for six nest predators sampled during 3,471 diurnal surveys in seven suburban neighborhoods in Columbus, Ohio, USA.

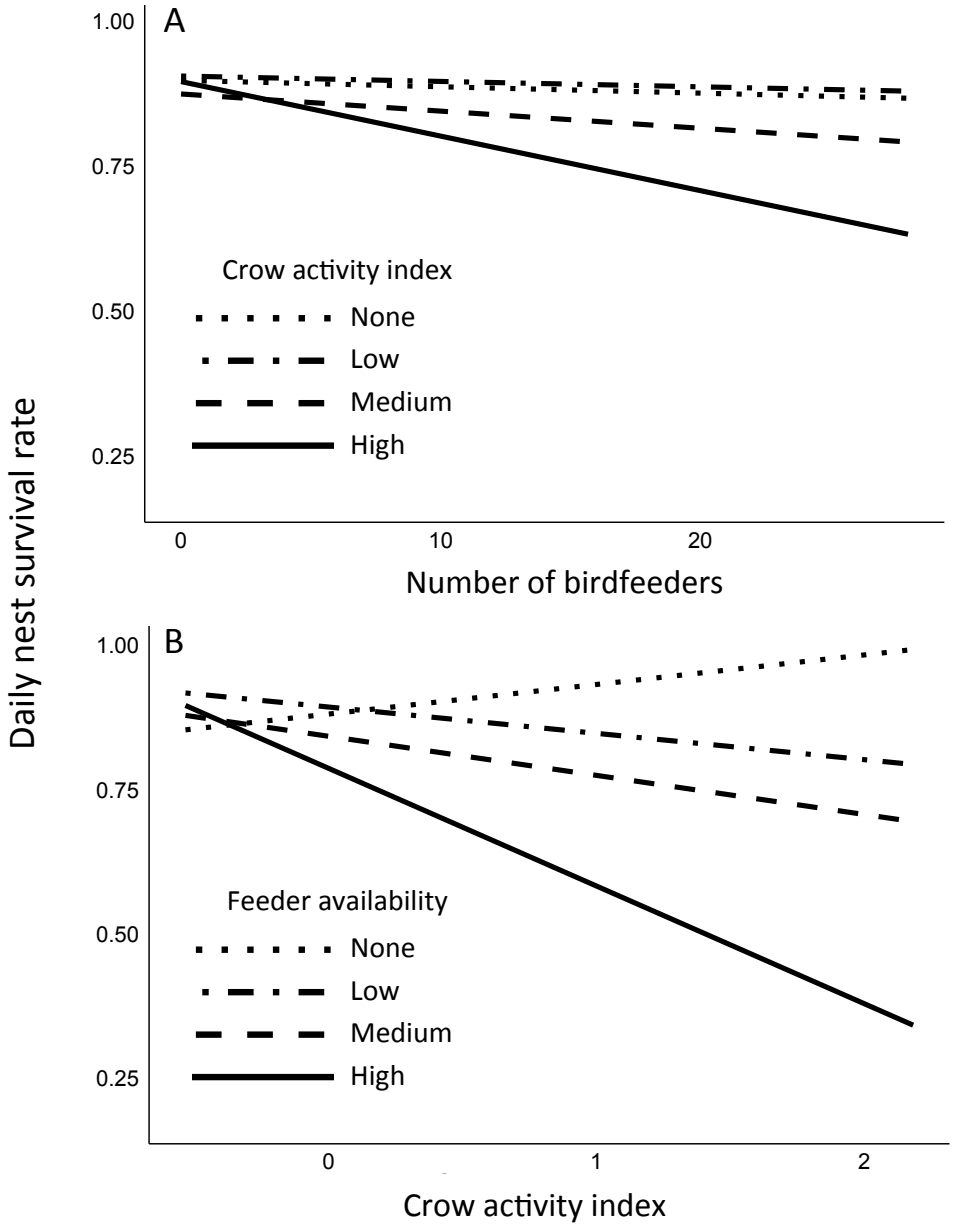

Figure 4.2. The relationship between bird feeders and daily nest survival (DSR) of robins in suburban neighborhoods depended on crow activity; bird feeders had negative effects on robin nest survival only in neighborhoods with medium to high levels of crow activity. For illustrative purposes, I graphed DSR at four levels of crow activity (A) and feeders (B): None= no observations, Low= minimum non-zero observation to first quartile, Medium= interquartile range, and High= above third quartile.

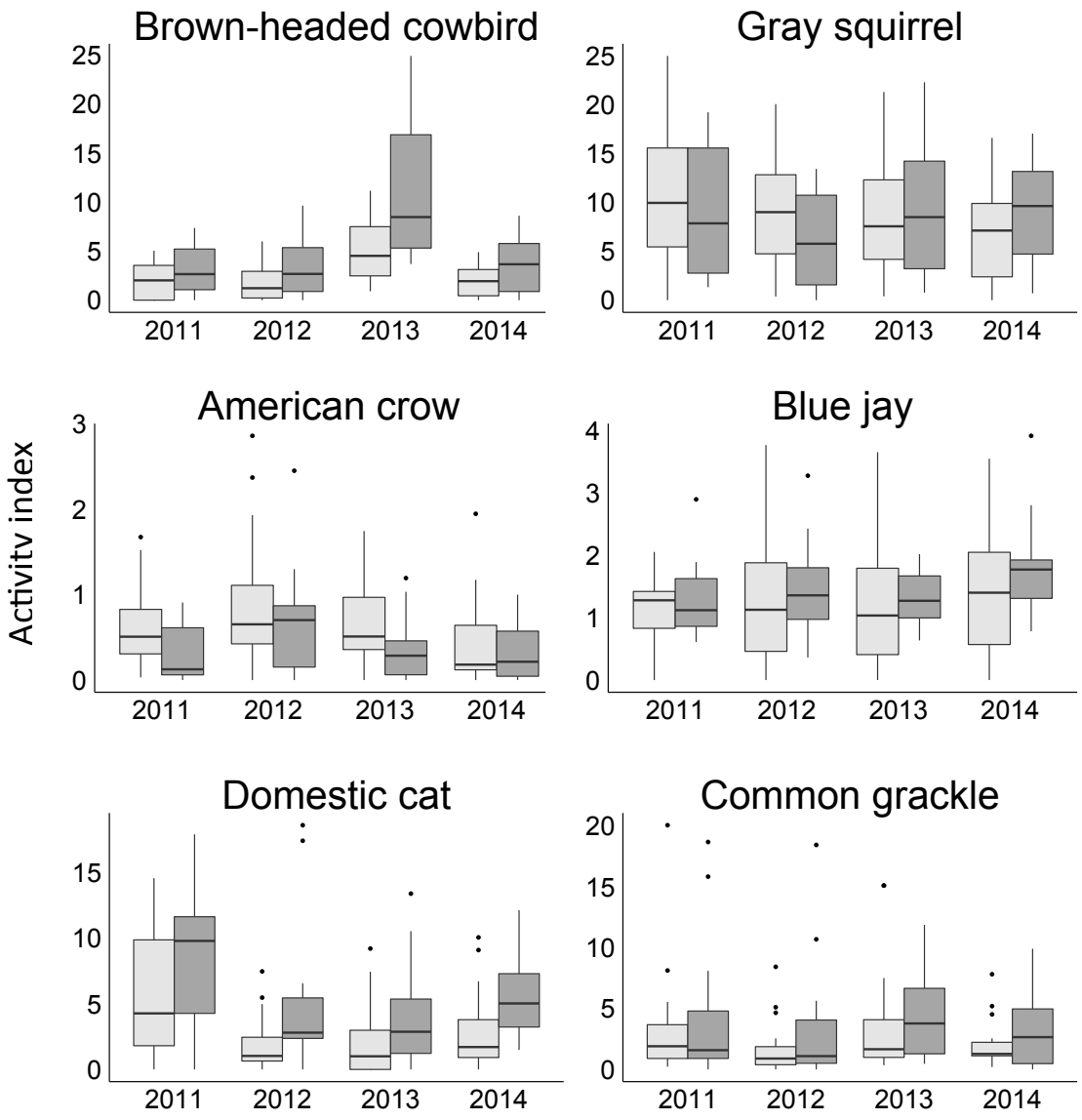

Figure 4.3. Diurnal activity of six nest predators was highly variable among years and treatments (control= light gray; experimental= dark gray) in seven suburban neighborhoods. Experimental neighborhoods were supplemented weekly with 9kg of birdseed during April- August 2013 and 2014.

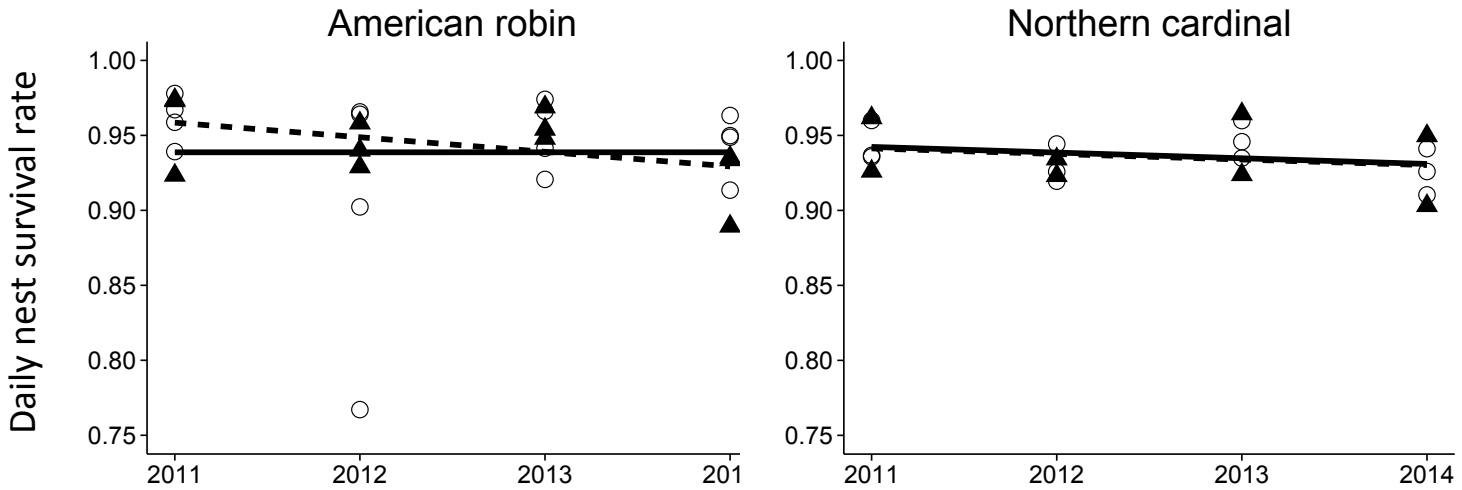

Figure 4.4. Daily nest survival rates for robins and cardinals were similar between control (hollow circles and solid line) and experimental neighborhoods (filled triangles and dashed line; *n*= 3). Experimental neighborhoods were supplemented weekly with 9kg of birdseed during April- August 2013 and 2014.

Chapter 5: Seeking success in the suburbs: Are some nest sites safer for backyard birds?

Abstract

Breeding birds should face strong pressure to select nesting sites safe from predators given that nest predation is the leading cause of nest failure. However, previous research has reported mixed findings regarding the effects of nest site characteristics on nest survival. Here I test how well vegetation characteristics of nest sites and features typical of the urban environment (i.e. roads, buildings, and anthropogenic foods) predict nest survival for two bird species that commonly nest in residential yards. During April-August 2011-2014, I monitored nests and assessed nest site characteristics of American robins, *Turdus migratorius*, and northern cardinals, *Cardinalis cardinalis*, breeding in seven suburban neighborhoods in the Columbus, Ohio metropolitan area. Nest site characteristics were not strong predictors of nest survival of cardinals, and height was the only significant predictor of nest survival for robins. I suggest that the lack of relationship between nest site characteristics and nest fate stem from a diverse predator community that effectively precludes any nest site from being predictably safe.

Introduction

Predation is a primary driver of avian reproductive success (Ricklefs, 1969) and avian community structure (Martin, 1995, 1988). Thus, breeding birds are expected to face strong pressure to select nesting sites safe from predation and significant research has been devoted to identifying which nest site characteristics have the strongest relationship with nest predation risk. Height of the nest, the extent to which foliage conceals the nest (nest concealment), and vegetation density around the nest may affect predator detection or access to nests, and thus may influence nest predation risk. However, the relationship between nest site characteristics and nest survival are not consistent and sometimes non-existent across studies (Braden, 1999; Burhans and Thompson, 1998, 2001; Filliater et al., 1994; Howlett and Stutchbury, 1996).

Generalizing the relationships between nest site characteristics and nest survival may be difficult because of contextual differences among studies, even where birds are nesting within the same land use type (e.g. forests, residential yards). Vegetation density in the area around the nest (i.e. in the nest patch) may be either positively or negatively associated with nest predation risk depending on the underlying mechanisms. Several studies have shown birds select nest sites (Knopf and Sedgwick, 1992) or territories (Leston and Rodewald, 2006) in dense vegetation, but nesting in dense vegetation may not confer a reproductive advantage in all cases. Nests may be less detectable to predators and experience higher survival rates where dense vegetation around nests offers a

multitude of potential nesting sites or helps to conceal nests (Chalfoun and Martin, 2009; Martin, 1993, 1988). Alternately, high understory stem density due to invasion of exotic shrubs may be associated with depressed nesting success for birds nesting in these substrates, perhaps because of enhanced search efficiency of nest predators when most nests are located in the same substrate (Borgmann and Rodewald, 2004; Rodewald et al., 2010; Schmidt and Whelan, 1999).

Differences in the suite of species responsible for nest depredations also may influence the effect of nest site characteristics on nest survival. For example, higher nests may be reduce risk of predation by terrestrial predators or be less detectable to species that use olfactory cues to detect nests (e.g. snakes; Burhans and Thompson, 1998). However, higher nesting sites may be riskier if other birds are responsible for the majority of depredations (Ocampo and Londoño, 2014). Differences in nest predation risk from avian versus mammalian predators may explain why nest height was positively associated with nest survival in some studies (Baghbadarani et al., 2014; Brown and Collopy, 2012; Etezadifar and Barati, 2015; Smith-Castro and Rodewald, 2010; Sperry et al., 2012), but not others (Braden, 1999; Filliater et al., 1994; Howlett and Stutchbury, 1996). In addition, the ability of nest concealment to decrease detectability to predators and subsequent nest predation risk likely depends on which species are most frequently responsible for nest depredations. For example, nest concealment may have a greater influence on nest survival where primary predators rely on visual cues to detect nests, e.g. birds (Clark and Nudds, 1991; Howlett and Stutchbury, 1996; Söderström et al., 1998).

Certain features associated with human developments may further mediate nest predation risk for birds breeding in cities. For example, proximity to roads and buildings, along with associated human use of these features, may attract certain predators or dissuade others. People and the behavioral responses of breeding birds to people (e.g. mobbing calls) may attract the attention of certain predators, such as corvids (Gutzwiller et al., 2002; McLean et al., 1986). At the same time, human presence may also spatially displace predator activity and create areas that are safe from certain predators (George and Crooks, 2006; Møller, 2012; Osborne and Osborne, 1980). For example, blackbird (*Turdus merula*) nests had higher survival when placed closer to buildings and paths on a university campus (Osborne and Osborne, 1980), and survival of American robins (*Turdus migratorius*) nests was positively related to pedestrian traffic in urban parks (Becker and Weisberg, 2015), presumably because human presence deterred predators.

The availability of abundant anthropogenic foods may influence nest predation risk in urban areas (Fischer et al., 2012). Anthropogenic foods may attract nest predators and concentrate their activity in areas where these subsidies are available (Bozek et al., 2007; Prange et al., 2004). If most nest predation is incidental, i.e. occurring opportunistically when a generalist predator is actively seeking a primary food source (Vickery et al., 1992), then predation risk may be more strongly related to food locations than to other nest site characteristics because these foods attract predators (Borgmann et al., 2013; Howlett and Stutchbury, 1996; Schmidt and Ostfeld, 2003). In particular, birds nesting near supplemental foods may experience depressed reproductive success

(Borgmann et al., 2013). In addition, in areas where anthropogenic foods attract terrestrial nest predators, such as opossums (*Didelphis virginiana*) or raccoons (*Procyon lotor*), increasing nest height may be more strongly associated with enhanced nest survival. Thus food availability may influence the effect of nest site characteristics on nest survival.

Few studies have addressed effects of nest vegetation characteristics and contextual features simultaneously (Borgmann et al., 2013; Filliater et al., 1994), and no prior study has concurrently addressed how vegetation characteristics, distances to roads and buildings, and food availability may interact to influence birds breeding in urban landscapes. Here I examine how nest site characteristics and anthropogenic food availability influence nest survival of American robins and northern cardinals, *Cardinalis cardinalis*. Specifically, I test whether nest height, nest concealment, vegetation density around nests, proximity to roads and proximity to buildings affect nest survival, and whether the effect of these nest site characteristics on nest survival is moderated by the availability of anthropogenic foods.

Methods

This research was conducted in seven residential neighborhoods (~ 3.5 ha) in the greater metropolitan area of Columbus, Ohio that had similar ranges of building density and landscape composition (see Rodewald and Shustack, 2008). With resident permission and along with trained technicians, I worked in 150 private yards in 2011, 173 in 2012,

151 in 2013, and 135 in 2014 (11- 32 yards per neighborhood; >50% area of each neighborhood). I monitored nests of American robin (robin) and northern cardinal (cardinal), the two most common open-cup nesting birds in the understory and midstory of residential yards within focal neighborhoods. Nests were checked every 1-4 d by either directly examining nest contents or by observing parental behavior from >10m from the nest to determine the nest stage (e.g. nest building, incubation, nestlings). To avoid exposing nests to predators as a result of my visits, I varied my routes to nests, checked contents briefly, and delayed checking nests if nest predators were observed in the vicinity.

I conducted surveys of nest site characteristics after each nest had fledged or failed. I measured nest height from the ground in meters and used a rangefinder to measure distances to nearest road and building. To estimate concealment, I used an ocular tube held 1m from the nest at the same height as the nest to estimate the percent of the nest that was covered by vegetation or other obstruction (e.g. part of a building for a robin nest on a drainpipe). I recorded the percent concealment in each of six directions: four cardinal directions, above, and below. Concealment of nests too high to reach was estimated from the best possible angle. To estimate vegetation density around the nest, I counted the number of trees >3 cm dbh within 11.3-m of the nest (nest patch). I also counted the number of times trees, shrubs and vines made contact ("woody hits") with a 3-m PVC pole placed perpendicular to the ground at 2-m intervals along two 20-m transects running north-south and east-west through the center of the nest patch, taking a

total of 20 measurements of woody hits (James and Shugart, 1970; Martin et al., 1997). I also recorded GPS data for each nest.

I surveyed each neighborhood monthly between April and August 2011-2014 to determine the locations and extent of anthropogenic foods. Surveys across all seven neighborhoods were conducted within the same 7-d period of the month. I created aerial maps for focal neighborhoods using GIS data of parcel boundaries, roads, and buildings from the Ohio Geographically Referenced Information Program (http://ogrip.oit.ohio.gov/). Trained observers spent 35-55 min per survey walking the neighborhood and identifying the locations of anthropogenic foods on these maps. Observers entered all properties where I had access for nest monitoring, and visually inspected remaining properties from a distance (i.e. on public property). For each food source detected, I recorded food type (i.e. type of birdseed, pet food, or trash), whether or not it was accessible to avian and/or mammalian nest predators. Hummingbird feeders were considered unavailable to nest predators, as were thistle-specific feeders, provided there was no seed under the feeder. I recorded each food item separately, including where there were multiple foods present at a single location (e.g. several bird feeders hanging from the same pole), which occurred for ~40% of foods. I used GPS units to record all the locations where food was accessible to avian and/or mammalian nests predators in yards where I had permission to access, and hand-digitized locations on aerial imagery for food locations on properties where I did not have permission to access. Every effort was made to survey the full extent of each neighborhood. However, because I was not

able to survey every yard due to access restrictions or visual obstruction (e.g. a privacy fence), results represent conservative estimates of anthropogenic food resources in these neighborhoods.

Analysis

I examined Spearman correlations to identify if measures of nest height, nest concealment, vegetation density, and distances to roads and buildings ("nest site characteristics") were correlated and to reduce the number of variables used for subsequent analyses by removing variables that reflected the same metric of interest (Knopf and Sedgwick, 1992). Nest concealment was averaged into a single metric because of high correlations (r= 0.6-0.9) between average concealment and the six individual estimates of concealment. The number of trees in the nest plot was positively associated with the number of woody hits summed across all 20 measurements (r =0.6). I used number of trees as the metric of vegetation density around the nest because counts of number of trees in the nest plot were less variable among observers than counts of woody hits and were not influenced by vegetation phonological development in relation to when the nest was active, both of which may introduce error (Burhans and Thompson, 1998). Distances to nearest road and building were not associated (-0.03) and both measures were retained for analysis. Spearman correlations indicated that none of the five remaining metrics of nest site characteristics (nest height, distance to road, distance to structure, concealment and number of trees within nest patch) were correlated more strongly than r=0.4.

I used kernel density estimation to define a value for anthropogenic food availability for each nest location using ArcMap 10 (ESRI, Redlands, CA). Kernel density estimation calculates a density of features (here, locations of birdseed, trash, and pet food available to avian and/or mammalian nest predators) in a defined area around those features, resulting in a raster surface which interpolates values for the feature of interest at all locations within the defined area (Silverman, 1986). I calculated the density of food locations within a 210-m radius from the center of nests found in each neighborhood, weighting each location by the number of food sources present at that location (Fig. D.1). This radius was selected because it encompassed all nests at each neighborhood. I created separate kernel density estimates for each month, year and neighborhood and extracted values for anthropogenic food for at each nest location in the month(s) the nest was active.

I used a logistic exposure model to estimate the daily nest survival rate of 92 robin nests and 134 cardinal nests monitored during April-August 2011-2014 in R 3.0.1 (R Core Development Team, 2013). The logistic exposure model is a generalized linear model that uses a binomial error distribution and a link function that estimates probability of nest survival between each visit to the nest, thereby eliminating potential bias due to different exposure periods (Shaffer and Burger, 2004). Nest fate at each nest check was modeled as either failing (0) or surviving (1) the nest-check interval.

I evaluated how well nest site characteristics and anthropogenic food predicted nests survival using three linear mixed models, testing robins and cardinals separately. In

the first model, I assessed the ability of nest height, number of trees within the nest plot, average nest concealment, distance to road, and distance to structure to predict nest survival. The second model was defined as the first model plus anthropogenic food availability as an additive term. In the third model, I allowed food to interact with any nest site variable that was a significant predictor of nest survival as per model 1. I used likelihood ratio tests to determine whether model fit improved if anthropogenic food availability was included as an additive term (i.e. comparing models 1 and 2) or in an interaction term (i.e. comparing models 2 and 3). All models included the random effect of neighborhood to account for neighborhood-level differences not captured by fixed effects. All predictor variables were centered and scaled to 1) prevent issues related to non-convergence of models that include variables on vastly different scales and 2) enhance interpretability of interaction terms (Schielzeth, 2010).

Results

For robins, nest height was the only nest site characteristic that had a significant influence on daily nest survival rate. Nest survival declined with increasing nest height (Fig. 5.1; estimate ± SE = -0.603 ± 0.2315; z= -2.605, partial p <0.01) and the probability that a robin nest would survive the 28-day nesting cycle was <10% for nests placed above 2m (Fig. 5.2). Model fit did not improve when food availability was included as an additive term (X^2_1 =0.030, p = 0.836) or allowed to interact with nest height (X^2_1 =2.773, p = 0.599).

For cardinals, none of the five nest site characteristics significantly predicted of daily nest survival rate, nor did adding food availability improve model fit (X^2_1 =0.543, p = 0.461). I did not test interaction terms of food and nest site characteristics for cardinals because none of the nest site characteristics were significantly associated with cardinal nest survival.

Discussion

Most nest site characteristics were not strongly associated with nest survival for either robins or cardinals. For cardinals, none of the predictors were related to daily nest survival, while for robins, nest height was the only significant predictor of nest survival. Findings in this study are consistent with other studies which similarly failed to find that nest site attributes were associated with nest fate (Braden, 1999; Burhans and Thompson, 1998, 2001; Filliater et al., 1994; Howlett and Stutchbury, 1996).

Why might nest site characteristics be only weakly related to nest survival? High rates of nest predation by a diverse predator guild may preclude the availability of predictably safe nesting sites, leading to a lack of association between nest site characteristics and nest survival (Filliater et al., 1994). For example, the effect of increasing nest height on nest predation risk differs depending on which species are the most common predators (Filliater et al., 1994; Newmark and Stanley, 2011). If avian predators are common, higher nests may be more vulnerable to predation because they

are more detectable or accessible. However, if terrestrial predators (e.g. mammals, snakes) are most frequently responsible for depredations, then this relationship is reversed: nest predation risk is higher for nests closer to the ground (Conkling et al., 2012; Sperry et al., 2012). Where both avian and mammalian species readily depredate nests, there may be no nest height that protects nests from both types of predators (but see Smith et al., 2014). Similarly, increasing nest concealment may protect nests only if certain species are dominant predators. For example, nest concealment may be more likely to influence predation risk in situations where avian species are primary nest predators, and nest concealment may be less associated with nest survival where mammalian or both mammalian and avian species are common predators (Clark and Nudds, 1991).

Differences in diversity and evenness of the suite of species documented depredating robin versus cardinal nests may explain why nest height was inversely related to nest survival for robins and no nest site characteristics were associated with nest survival for cardinals. In this study system, relatively few species have been documented depredating robin nests (n=4), and the majority of depredations (53%) are attributed to American crows, *Corvus brachyrhynchos*, with *Accipiter* spp. accounting for another 13% of depredations (Ch. 2). Thus, robin nesting higher in vegetation may be more vulnerable to predation than those closer to the ground because most depredated nests suffer losses to avian species, which are effective at finding nests in the canopy (Marzluff et al., 2001). In contrast, cardinal nests are depredated by a wider suite of

species (11 species documented depredating nests in yards), and no individual avian or mammalian species dominates (Ch. 2; see also Rodewald and Kearns, 2011). Results of this study suggest that future work that addresses factors influencing avian nest survival should identify the species responsible for depredations when also considering the effect of individual nest site characteristics (Reidy and Thompson, 2012).

In addition, nest site characteristics may not be strongly associated with nest survival in situations where factors affecting nest fate operate at larger spatial scales than the nest patch (Braden, 1999). For example, when crow activity and bird feeder availability were assessed at the neighborhood level, I found negative effects of high crow activity and many bird feeders on robin nest survival (Ch. 4). However, anthropogenic food at the nest patch (as measured here) may not have been strongly associated with nest survival for robins if crows respond to food availability at coarser spatial scales.

One limitation to our use of distance to roads or buildings as a predictor of nest survival is that these metrics did not measure human activity directly (c.f. Becker and Weisberg, 2015), and thus may not have accurately captured variation in human activity near robin and cardinal nests. Also, effects of roads and buildings on nest survival may depend on time of day if nest predators are displaced temporally as opposed to spatially by human presence and shift periods of peak activity to times when humans are not active (George and Crooks, 2006). Alternately, the effect of buildings and roads on nest survival may only be measurable beyond a certain threshold. However, there were a wide range of

distances to buildings (0-47m) and roads (0-74m) represented among the nests included in this analysis.

Although birds should face strong selective pressure to choose nesting sites that offer protection from nest predators because predation is the leading cause of nest failure, where predator communities are diverse there may be no predictable locations that protect from all types of nest predators. The diverse suite of species known to depredate nests in my study system (Ch. 2) may be the reason I found no association between nest site characteristics and cardinal nest survival and nest height as the only significant predictor of robin nests survival. Future research examining the relationship among nest site characteristics and nest survival should identify which species are responsible for nest depredation events to determine whether this pattern is consistent across study systems.

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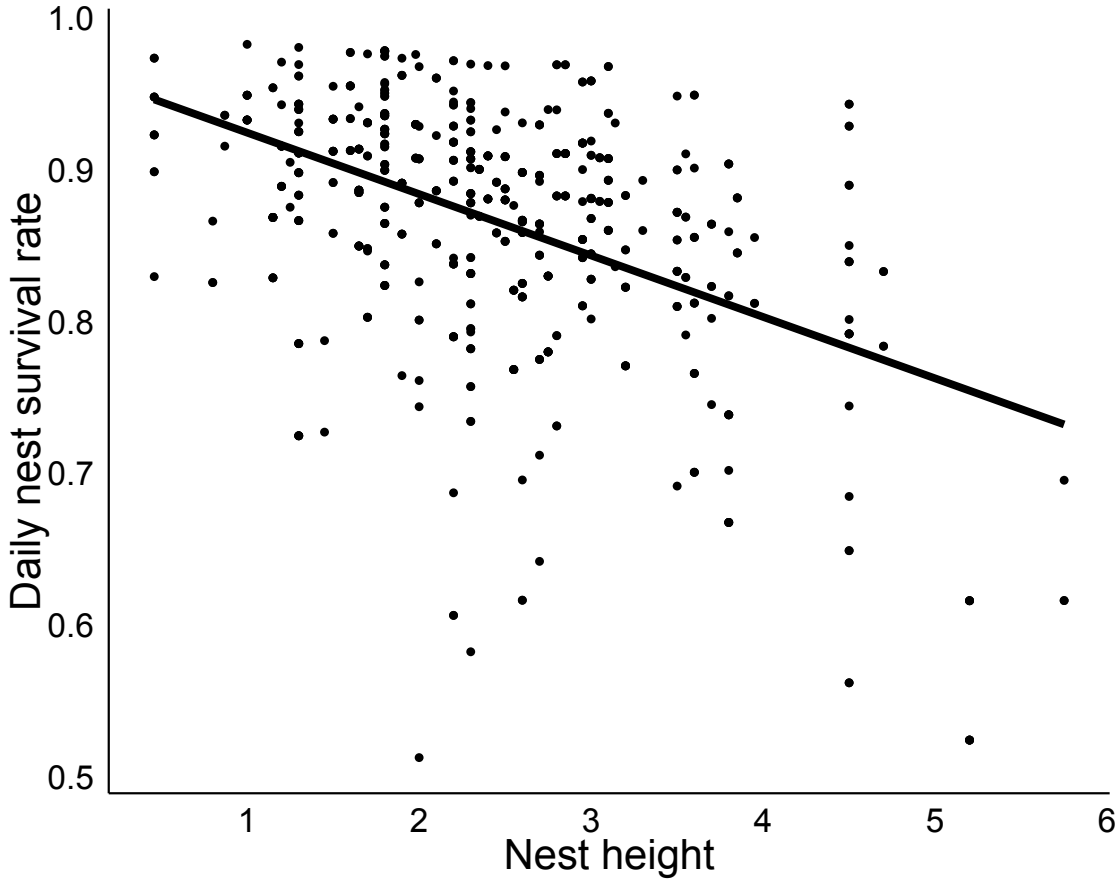

Figure 5.1. Daily nest survival rate for robins decreased with increasing nest height (m) for 92 robin nests in residential yards monitored during April-August 2011-2014 in the Columbus, Ohio metropolitan area.

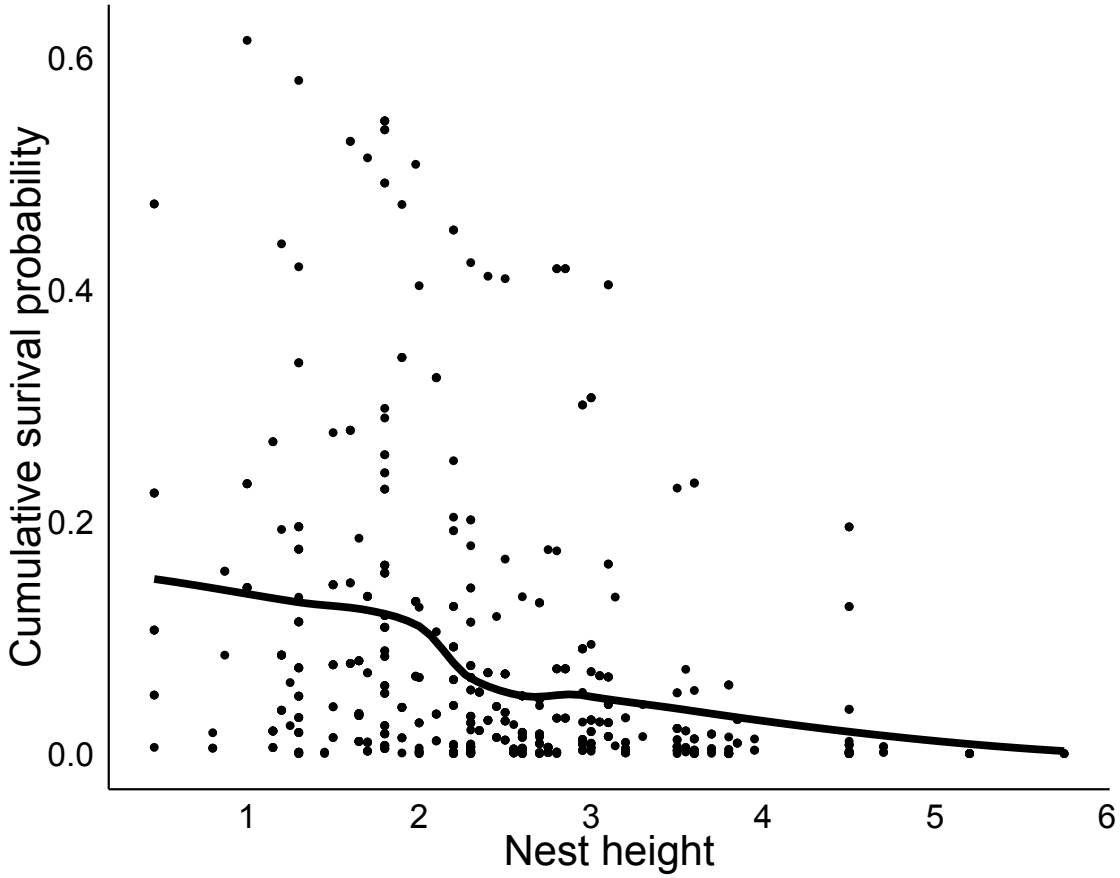

Figure 5.2. Cumulative survival probability (i.e. daily nest survival rate^28) for robin nests decreases with increasing nest height (m). The solid black line represents the loess best-fit line.

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Appendix A: Supplementary material for Chapter 2

Table A.1. Daily nest survival estimates (DSR) and 95% confidence intervals (CI) for American robin (*Turdus migratorius*) nests monitored in seven pairs of forest parks (Reserve) and residential yards (Matrix) in the Columbus, Ohio metropolitan area. *N*= number of nests.

Habitat	Year	Site	DSR	95% CI	*N*
Reserve	2011	Casto	0.970	(0.912 - 0.969)	21
		Elk Run	0.927	(0.948 - 0.985)	19
		Kenny	0.902	(0.760 - 0.902)	12
		Rush Run	0.985	(0.856 - 0.97)	8
		Tuttle	0.969	(0.821 - 0.927)	11
	2012	Casto	0.964	(0.859 - 0.950)	12
		Elk Run	0.983	(0.895 - 0.978)	8
		Rush Run	0.985	(0.790 - 0.951)	7
		Tuttle	0.991	(0.897 - 0.965)	15
		Woodside	0.967	(0.900 - 0.983)	6
	2013	Casto	0.985	(0.926 - 0.990)	6
		Kenny	0.985	(0.868 - 0.969)	8
		Tuttle	0.983	(0.958 - 0.994)	12
	2014	Casto	0.951	(0.901 - 0.973)	10
		Kenny	0.978	(0.896 - 0.970)	13
		Rush Run	0.950	(0.856 - 0.966)	7
		Tuttle	0.965	(0.837 - 0.935)	8
		Woodside	0.883	(0.848 - 0.961)	7
Matrix	2011	Casto	0.960	(0.947 - 0.991)	12
		Cherry	0.934	(0.844 - 0.964)	5
		Elk Run	0.978	(0.955 - 0.985)	24
		Kenny	0.959	(0.889 - 0.967)	12
		Rush Run	0.978	(0.903 - 0.983)	8
		Tuttle	0.973	(0.931 - 0.985)	11
		Woodside	0.990	(0.952 - 0.985)	20
	2012	Casto	0.969	(0.941 - 0.978)	23
		Cherry	0.994	(0.878 - 0.960)	11
		Elk Run	0.971	(0.937 - 0.973)	28
		Kenny	0.977	(0.858 - 0.934)	20
		Rush Run	0.980	(0.590 - 0.883)	6
		Tuttle	0.945	(0.946 - 0.978)	21
		Woodside	0.984	(0.913 - 0.959)	22

continued

Table A.1, continued

2013	Casto	0.964	(0.958 - 0.984)	29
	Cherry	0.981	(0.910 - 0.977)	14
	Elk Run	0.966	(0.925 - 0.964)	30
	Kenny	0.961	(0.886 - 0.945)	27
	Rush Run	0.935	(0.886 - 0.971)	10
	Tuttle	0.973	(0.944 - 0.980)	21
	Woodside	0.970	(0.951 - 0.981)	31
2014	Casto	0.957	(0.927 - 0.966)	28
	Cherry	0.934	(0.820 - 0.934)	11
	Elk Run	0.978	(0.912 - 0.950)	38
	Kenny	0.967	(0.922 - 0.967)	24
	Rush Run	0.966	(0.835 - 0.957)	5
	Tuttle	0.950	(0.939 - 0.978)	20
	Woodside	0.952	(0.914 - 0.952)	40

Table A.2. Daily nest survival estimates (DSR) and 95% confidence intervals (CI) for Northern cardinal (*Cardinalis cardinalis*) nests monitored in seven pairs of forest parks (Reserve) and residential yards (Matrix) in the Columbus, Ohio metropolitan area. *N*= number of nests.

Habitat	Year	Site	DSR	95% CI	*N*
Reserve	2011	Casto	0.964	(0.910 - 0.956)	31
		Cherry	0.956	(0.911 - 0.964)	19
		Elk Run	0.951	(0.933 - 0.969)	36
		Kenny	0.969	(0.874 - 0.913)	83
		Rush Run	0.961	(0.895 - 0.934)	63
		Tuttle	0.934	(0.922 - 0.961)	38
		Woodside	0.913	(0.905 - 0.951)	31
	2012	Casto	0.982	(0.852 - 0.926)	18
		Cherry	0.981	(0.909 - 0.975)	10
		Elk Run	0.955	(0.842 - 0.943)	10
		Kenny	0.956	(0.857 - 0.918)	41
		Rush Run	0.956	(0.864 - 0.926)	35
		Tuttle	0.975	(0.876 - 0.936)	29
		Woodside	0.943	(0.920 - 0.966)	24
	2013	Casto	0.926	(0.856 - 0.951)	10
		Cherry	0.966	(0.876 - 0.945)	16
		Kenny	0.936	(0.916 - 0.961)	31
		Rush Run	0.926	(0.920 - 0.972)	19
		Tuttle	0.918	(0.914 - 0.951)	46
		Woodside	0.971	(0.909 - 0.972)	11
	2014	Casto	0.964	(0.907 - 0.979)	12
		Cherry	0.949	(0.935 - 0.993)	8
		Elk Run	0.943	(0.910 - 0.967)	18
		Kenny	0.948	(0.873 - 0.925)	36
		Rush Run	0.951	(0.893 - 0.940)	35
		Woodside	0.972	(0.897 - 0.979)	9

continued

Table A.2, continued

Matrix	2011	Cherry	0.945	(0.881 - 0.955)	17
		Kenny	0.972	(0.909 - 0.956)	31
		Rush Run	0.961	(0.907 - 0.956)	30
		Tuttle	0.951	(0.912 - 0.982)	8
		Woodside	0.962	(0.924 - 0.981)	13
	2012	Cherry	0.984	(0.887 - 0.949)	25
		Kenny	0.981	(0.895 - 0.948)	33
		Rush Run	0.977	(0.887 - 0.943)	32
		Tuttle	0.948	(0.895 - 0.971)	12
		Woodside	0.965	(0.884 - 0.964)	13
	2013	Casto	0.956	(0.852 - 0.962)	5
		Cherry	0.993	(0.889 - 0.948)	24
		Elk Run	0.979	(0.918 - 0.981)	10
		Kenny	0.979	(0.905 - 0.956)	28
		Rush Run	0.967	(0.916 - 0.965)	25
		Tuttle	0.940	(0.930 - 0.977)	16
		Woodside	0.925	(0.922 - 0.984)	9
	2014	Cherry	0.975	(0.849 - 0.939)	17
		Kenny	0.967	(0.880 - 0.934)	37
		Rush Run	0.939	(0.894 - 0.949)	31
		Tuttle	0.949	(0.898 - 0.967)	12
		Woodside	0.934	(0.901 - 0.975)	9

Table A.3. Documented nest depredations on Northern cardinal (*Cardinalis cardinalis*) nests in seven forest parks in the Columbus, Ohio metropolitan area. Time is unknown for two depredations recorded by video cameras without date/time stamps. Scientific names for predators are listed in Table 2.1.

Nest ID	Site	Date	Time	Nest Stage	Predator
0701069	Cherry	6/23/07	23:55	Nestlings	*Accipiter* sp.
0710196	Kenny	8/9/07	15:30	Nestlings	Unidentified bird
0710204	Rush Run	8/15/07	15:00	Nestlings	Domestic cat
0710204	Rush Run	8/19/07	3:00	Nestlings	Unidentified mammal
0801005	Kenny	4/24/08	18:15	Eggs	Common grackle
0801010	Elk Run	4/28/08	15:15	Eggs	Brown-headed cowbird
0804008	Rush Run	5/3/08	21:30	Eggs	Raccoon
0803012	Elk Run	5/5/08	10:15	Nestlings	Common grackle
0805020	Cherry	5/19/08	6:30	Nestlings	Unidentified mammal
0804022	Rush Run	5/19/08	19:45	Nestlings	American crow
0804019	Rush Run	5/24/08	10:30	Nestlings	Raccoon
0802025	Casto	5/31/08	0:00	Nestlings	Barred owl
0804041	Kenny	6/7/08	5:15	Nestlings	Domestic cat
0801074	Cherry	7/27/08	23:15	Nestlings	Raccoon
0904001	Woodside	4/14/09	11:30	Eggs	Unidentified bird
0904018	Woodside	4/18/09	11:45	Eggs	Brown-headed cowbird
0904013	Casto	4/22/09	9:30	Eggs	Eastern gray squirrel
0901010	Rush Run	4/22/09	14:15	Eggs	American crow
0901029	Rush Run	4/25/09	6:45	Eggs	Northern Cardinal
0905008	Elk Run	4/26/09	11:45	Nestlings	Brown-headed cowbird
0903015	Woodside	4/28/09	9:15	Eggs	Brown-headed cowbird
0903016	Woodside	4/30/09	16:30	Eggs	Unidentified mammal
0901020	Kenny	4/30/09	6:15	Nestlings	Brown-headed cowbird
0901033	Kenny	5/1/09	15:00	Eggs	Brown-headed cowbird
0904005	Cherry	5/1/09	21:00	Nestlings	Unidentified mammal
0901055	Kenny	5/21/09	12:45	Nestlings	Blue jay
0902051	Tuttle	5/29/09	2:30	Nestlings	Unidentified mammal
0901099	Rush Run	6/20/09	16:00	Nestlings	Cooper's hawk
0906150	Elk Run	6/23/09	8:00	Eggs	Common grackle

continued

Table A.3, continued

0901120	Kenny	7/3/09	15:45	Eggs	Brown-headed cowbird
0909033	Cherry	7/20/09	5:30	Nestlings	Raccoon
0913008	Kenny	8/8/09	17:30	Eggs	American crow
0913008	Kenny	8/12/09	16:15	Eggs	Unidentified squirrel
1007018	Rush Run	4/14/10	14:15	Eggs	Brown-headed cowbird
1007006	Rush Run	4/18/10	15:45	Eggs	Eastern gray squirrel
1001005	Tuttle	4/22/10	7:45	Eggs	Brown-headed cowbird
1005005	Elk Run	4/24/10	8:15	Nestlings	Brown-headed cowbird
1007017	Rush Run	4/27/10	5:00	Eggs	Raccoon
1005020	Elk Run	5/3/10	11:45	Eggs	Common grackle
1007056	Rush Run	5/7/10	15:45	Eggs	Blue jay
1002088	Rush Run	5/27/10	7:30	Eggs	Eastern gray squirrel
1003070	Cherry	6/1/10	16:30	Eggs	Gray Domestic catbird
1003070	Cherry	6/1/10	20:30	Eggs	Unidentified snake
1002107	Kenny	6/11/10	10:15	Eggs	Eastern chipmunk
1002107	Kenny	6/11/10	15:15	Eggs	American crow
1006005	Rush Run	6/12/10	22:45	Nestlings	Raccoon
1001082	Tuttle	6/14/10	14:15	Eggs	Brown-headed cowbird
1002122	Kenny	6/18/10	9:30	Nestlings	*Accipiter* sp.
1002119	Kenny	6/25/10	Unknown	Eggs	Gray catbird
1013026	Rush Run	7/13/10	0:03	Eggs	Unidentified mammal
1006025	Rush Run	7/22/10	Unknown	Nestlings	Domestic cat
1002155	Rush Run	8/6/10	6:15	Nestlings	Cooper's hawk
1002155	Rush Run	8/9/10	10:30	Nestlings	Cooper's hawk
1008010	Tuttle	8/21/10	22:30	Nestlings	Virginia opossum
1001106	Tuttle	8/26/10	6:15	Nestlings	Virginia opossum

Table A.4. Documented depredations on cardinal and robin nests in seven residential neighborhoods in the Columbus, Ohio metropolitan area. Time is listed as AM for depredations that were visually observed during regular nest checks; remaining depredations were recorded with video cameras. The same cat was responsible for the three depredations on nest 1113098; this was tallied as a single instance of cat depredation in Table 2.1.

Species	Nest ID	Site	Date	Time	Nest Stage	Predator
Northern cardinal,	1113016	Woodside	4/20/11	AM	Eggs	Brown-headed cowbird
Cardinalis cardinalis	1106030	Woodside	4/30/11	20:13	Eggs/Nestlings	Cooper's hawk
	1113116	Kenny	6/2/11	15:34	Nestlings	Eastern chipmunk
	1106119	Tuttle	6/9/11	21:13	Eggs	Domestic cat
	1113098	Cherry	6/14/11	0:54	Eggs	Domestic cat
	1113098	Cherry	6/14/11	23:17	Eggs	Domestic cat
	1113098	Cherry	6/15/11	1:27	Eggs	Domestic cat
	1106166	Rush Run	7/4/11	17:36	Eggs	Brown-headed cowbird
	1113143	Kenny	7/19/11	12:33	Eggs	Eastern gray squirrel
	1106170	Cherry	7/24/11	4:28	Nestlings	Rat
	1113140	Kenny	7/29/11	19:02	Nestlings	Eastern gray squirrel
	1213062	Rush Run	4/23/12	15:36	Eggs	American crow
	1213092	Rush Run	5/14/12	AM	Nestlings	Domestic cat
	1206046	Woodside	5/14/12	19:05	Nestlings	Domestic cat
	1213151	Cherry	6/21/12	3:15	Nestlings	Raccoon
	1206171	Cherry	7/15/12	2:32	Nestlings	Virginia opossum
	1313050	Rush Run	5/1/13	10:57	Eggs	American crow
	1313054	Casto	5/17/13	12:18	Eggs	Blue jay

continued

Table A.4, continued

	1305080	Cherry	5/26/13	16:23	Eggs	American crow
	1313100	Cherry	5/29/13	2:12	Eggs	Domestic cat
	1305094	Woodside	6/7/13	AM	Eggs/Nestlings	Eastern gray squirrel
	1313113	Tuttle	6/15/13	11:21	Eggs	Eastern gray squirrel
	1306105	Cherry	6/22/13	21:41	Eggs/Nestlings	Unidentified snake
	1305131	Kenny	7/8/13	4:15	Eggs	Virginia opossum
	1413086	Cherry	5/7/14	1:55	Eggs	Domestic cat
	1405053	Cherry	5/20/14	12:53	Eggs	Brown-headed cowbird
	1405053	Cherry	5/20/14	12:53	Eggs	Brown-headed cowbird
American robin, *Turdus migratorius*	1106033	Kenny	4/28/11	AM	Eggs	American crow
	1113049	Tuttle	5/29/11	3:26	Nestlings	Raccoon
	1113087	Cherry	6/5/11	1:38	Eggs	Domestic cat
	1106130	Elk Run	6/30/11	7:05	Nestlings	American crow
	1206014	Casto	4/11/12	10:49	Eggs	American crow
	1206017	Woodside	4/27/12	AM	Nestlings	American crow
	1213075	Kenny	5/15/12	9:00	Eggs	American crow
	1213075	Kenny	5/18/12	18:20	Eggs	American crow
	1213075	Kenny	5/27/12	14:40	Nestlings	American crow
	1213131	Woodside	6/22/12	2:02	Nestlings	Unidentified mammal
	1406011	Elk Run	4/13/14	4:35	Eggs	Domestic cat
	1406001	Elk Run	4/26/14	AM	Nestlings	American crow
	1413011	Elk Run	5/1/14	3:40	Nestlings	Raccoon
	1406040	Elk Run	6/1/14	14:03	Nestlings	*Accipiter* sp.
	1413208	Elk Run	6/30/14	9:12	Nestlings	*Accipiter* sp.

Appendix B: Supplementary material for Chapter 3

Table B.1. Mantel test autocorrelation coefficients for activity level of six nest predator species within seven residential neighborhoods in the Columbus, Ohio metropolitan area, 2011-2012. Thirty-meter radius surveys were conducted at eight locations in each neighborhood and activity was defined as the mean number of detections per survey. Significant autocorrelation at $p<0.5$ is indicated by *, while $p<0.01$ is indicated by **. Where no year is indicated, activity was pooled between years.

Predator Species	Neighborhood	Correlation	p-value (left tailed)	p-value (right tailed)
Eastern gray squirrel	Casto	0.43	0.08	0.92
	Cherry	-0.09	0.62	0.38
	Elk Run	0.26	0.20	0.80
	Kenny	-0.32	0.96	0.037*
	Rush Run	-0.09	0.58	0.42
	Tuttle	-0.17	0.80	0.20
	Woodside	0.12	0.30	0.70
Common grackle	Casto	0.27	0.12	0.88
	Cherry	-0.05	0.53	0.47
	Elk Run	0.11	0.39	0.61
	Kenny	-0.08	0.62	0.38
	Rush Run	0.51	0.02	0.98
	Tuttle	0.06	0.34	0.66
	Woodside	-0.08	0.64	0.36
Brown-headed cowbird	Casto	0.39	0.07	0.93
	Cherry	-0.06	0.52	0.48
	Elk Run	0.04	0.49	0.51
	Kenny	-0.11	0.69	0.31
	Rush Run	0.28	0.17	0.83
	Tuttle	0.12	0.23	0.77
	Woodside	-0.11	0.70	0.30

continued

Table B.1, continued

Blue jay	Casto	0.53	0.010*	0.99
	Cherry	0.42	0.018*	0.98
	Elk Run	0.12	0.36	0.65
	Kenny	-0.21	0.84	0.16
	Rush Run	0.54	0.02	0.98
	Tuttle	0.27	0.09	0.91
	Woodside	0.21	0.15	0.85
Cat, 2011	Casto	0.23	0.19	0.81
	Cherry	-0.15	0.70	0.30
	Elk Run	0.3	0.14	0.86
	Kenny	-0.05	0.54	0.46
	Rush Run	0.08	0.40	0.60
	Tuttle	-0.18	0.81	0.19
	Woodside	-0.22	0.73	0.28
Cat, 2012	Casto	0.25	0.19	0.81
	Cherry	-0.18	0.75	0.25
	Elk Run	0.18	0.32	0.68
	Kenny	0.41	0.024*	0.98
	Rush Run	-0.15	0.70	0.31
	Tuttle	-0.18	0.84	0.16
	Woodside	-0.07	0.61	0.39

Table B.2. Mantel test autocorrelation coefficients for percent woody cover within seven residential neighborhoods in the Columbus, Ohio metropolitan area, 2011-2012. Percent woody cover within a 30 m radius of eight locations in each neighborhood was identified using random sampling of aerial images. Significant autocorrelation at $p<0.5$ is indicated by *.

Neighborhood	Correlation	*p*-value (left tailed)	*p*-value (right tailed)
Casto	0.42	0.10	0.90
Cherry	-0.25	0.96	0.04*
Elk Run	-0.08	0.52	0.48
Kenny	0.11	0.27	0.73
Rush Run	0.06	0.37	0.63
Tuttle	0.13	0.21	0.79
Woodside	0.39	0.04*	0.96

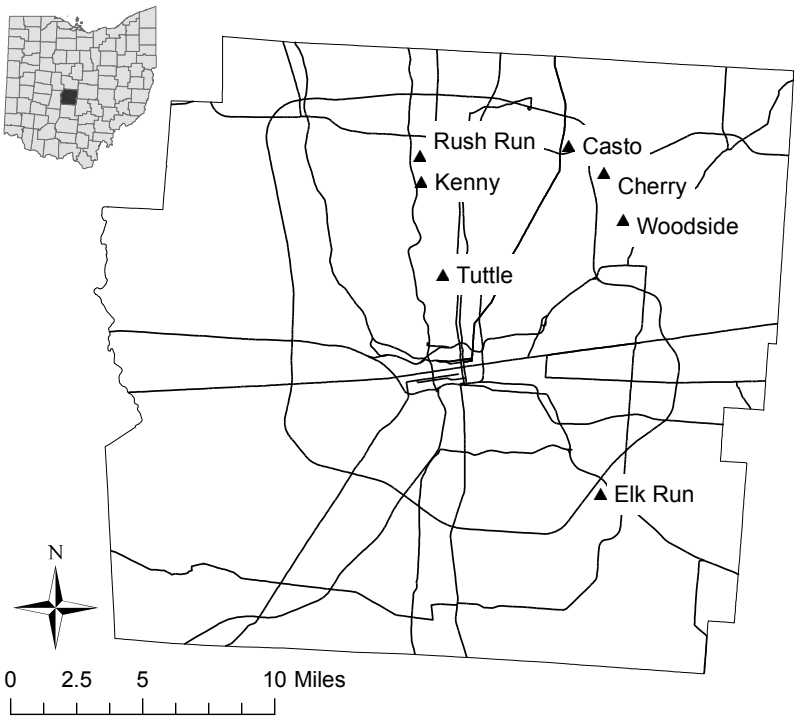


Figure B.1. Locations of seven focal neighborhoods in the greater metropolitan area of Columbus, Ohio, USA.

Appendix C: Supplementary material for Chapter 4

Figure C.1. Aerial map and locations of robin (crosses) and cardinal (circles) nests monitored during April-August 2011-2014 in Casto neighborhood, where 22 yards were included in 2011, 21 in 2012 and 2013, and 18 in 2014.

Figure C.2. Aerial map and locations of robin (crosses) and cardinal (circles) nests monitored during April-August 2011-2014 in Cherry neighborhood, where 13 yards were included in 2011 and 2012, 12 in 2013 and 11 in 2014.

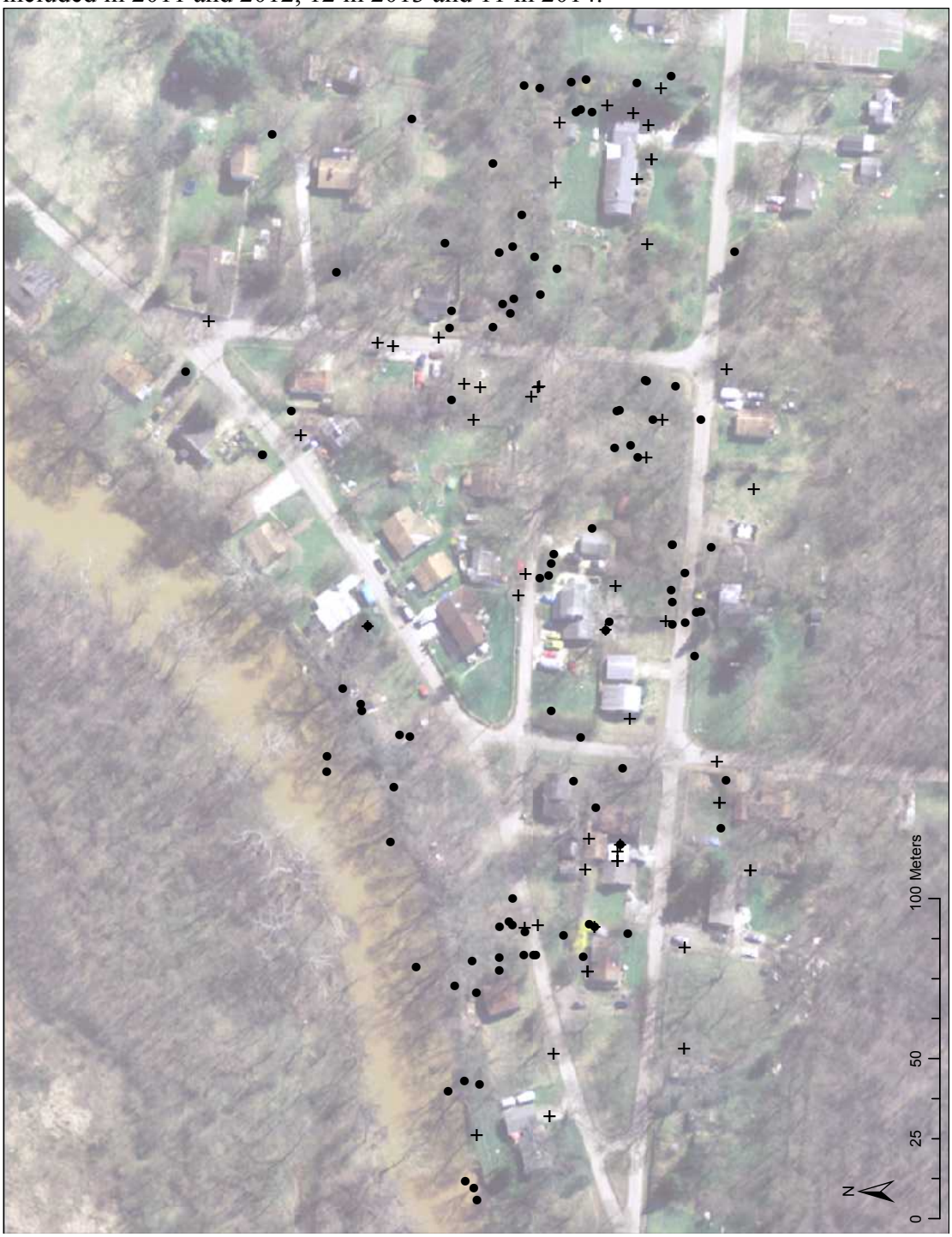


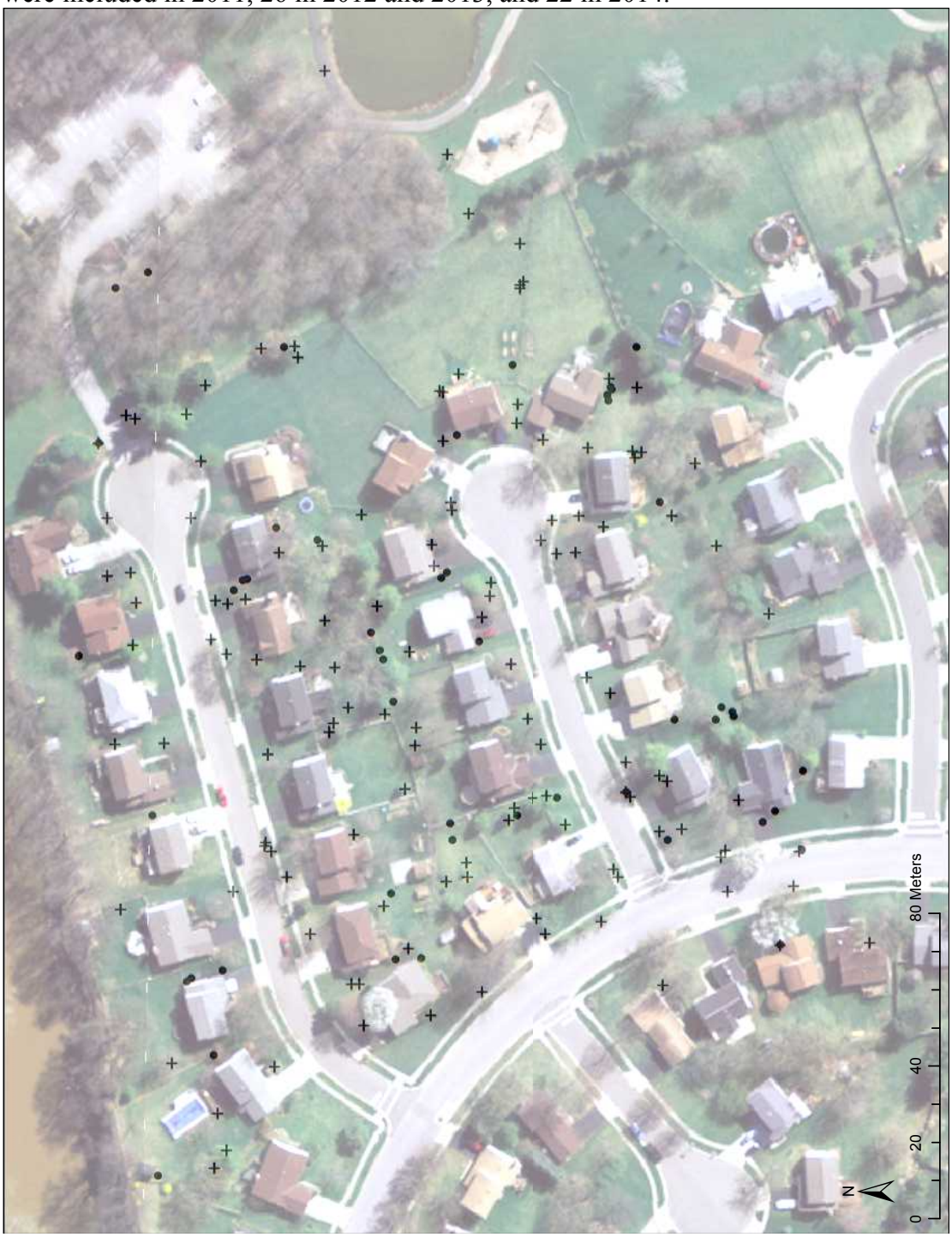
Figure C.3. Aerial map and locations of robin (crosses) and cardinal (circles) nests monitored during April-August 2011-2014 in Elk Run neighborhood where 17 yards were included in 2011, 16 in 2012, 20 in 2013 and 15 in 2014.

Figure C.4. Aerial map and locations of robin (crosses) and cardinal (circles) nests monitored during April-August 2011-2014 in Kenny neighborhood where 18 yards were included in 2011, 32 in 2012, 27 in 2013 and 22 in 2014.

Figure C.5. Aerial map and locations of robin (crosses) and cardinal (circles) nests monitored during April-August 2011-2014 in Rush Run neighborhood where 19 yards were included in 2011, 18 in 2012, 22 in 2013 and 20 in 2014.

Figure C.6. Aerial map and locations of robin (crosses) and cardinal (circles) nests monitored during April-August 2011-2014 in Tuttle neighborhood where 26 yards were included in 2011 and 2012, 23 in 2013 and 27 in 2014.

Figure C.7. Aerial map and locations of robin (crosses) and cardinal (circles) nests monitored during April-August 2011-2014 in Woodside neighborhood where 17 yards were included in 2011, 26 in 2012 and 2013, and 22 in 2014.



Appendix D: Supplementary material for Chapter 5

Figure D.1. Example of a kernel density estimate map representing availability of anthropogenic food resources (circles) at Kenny in April 2011, with the size of circles representing the number of food resources available at that location (range: 1 to 6).